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ABSTRACT

This Chautauqua-type short course in human evolution is divided into two parts: The Biochemical Evidence for Human Evolution, and the Fossil Evidence for Human Evolution. The first part covers the comparison of macromolecular differences between species. This includes comparison of DNA base-ratios and amino acid substitution in enzymes and other peptides. Electrophoresis and immunological techniques are discussed. In the second part, the fossil evidence for human evolution found in South Africa, East Africa, the Lake Turkana Basin, and Northern Kenya is presented. In addition, problems in dating fossils and in interpretation are discussed. (BB)

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Human Origins:
Problems in the Interpretation of New Evidence

by ALAN J. ALMQUIST and JOHN E. CRONIN

AAAS STUDY GUIDES ON CONTEMPORARY PROBLEMS

A part of the

NSF CHAUTAUQUA - TYPE SHORT COURSES FOR COLLEGE TEACHERS PROGRAM

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Third Edition
(Unedited Copy)

HUMAN ORIGINS:

Problems in the Interpretation of New Evidence

by

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ERRATA

Preface		Line 25	Change fourth edition to third edition.
Page	4	Line 4	Correct spelling of controversies.
	5	Line 15	Correct spelling of proteins.
	7	Last line	Correct spelling of vary.
	13	Line 4	Correct spelling of Nei.
	15	Line 1	Correct spelling of antibody.
		Line 24	Insert produced in response to a.
	19	Line 10	Correct spelling of stochastic.
		Line 14	Correct spelling of (covarions).
		Line 21	Change 6 m.y. to 600 m.y.
	20	Line 1	Change 2.5 - 3 - 0 m.y. to 2.5 - 3.0 m.y.
	22	Line 15	Correct spelling LHTA to OHTA.
	27	Line 6	Correct spelling of separated.
	29	Line 1 Fig 1-6	Change as to has.
Page	136	Line 20.	After White and Harris change (in press) to (1977).
		Line 26.	Correct spelling of reversed.
Page	155		Following SK 45 ad: SK 46, SK 47, SK 48, SK 49 and following SK 50 add: SK 52-54.
Page	157		After SK 83 add: Early adult, severely damaged cranium, palate, upper left dentition. 1949-1950 Trans. Mus.Mem. 9:41.
Page	159		After SK 846 add: rt M_1 1952 Trans. Mus.Mem. 9:69-71. After SK 847 add: elderly adult cranium 1952 unpublished. After SK 848 add: auditory region w/ ex. auditory aperture and glenoid fossa 1952 unpublished. After SK 859 add: juvenile, major portion of occipital and parietal 1952 unpublished.
Page	160		After SK 877 add: maxilla w/ rt P4M1M2 1952 unpublished. After SK 881 add: maxilla w/ left P3P4M1 1952 unpublished. After SK 882 add: upper left M (same as 881?) 1952 unpublished.

Page 162 Following SK 14003 add:

SK 46	Adult cranium w/ left half of braincase portion of face post canine dentition	1949	Trans. Mus. Mem. 6: 14-15
Sk 47	Adolescent cranium, crushed w/ base and palate M^3 emerging	1949	Trans. Mus. Mem. 6: 28-30
SK 48	Adult cranium, base, occipital and palante, inc. upper dentition	1949-50	Trans.Mus.Mem. 6: 10-13
SK 49	Adult cranium, crushed w/ separate occipital, upper dentition	1949-50	Nature 174: 262-63
SK 52	Adolescent cranium w/ lower part of face and rt side	1949-50	Trans.Mus.Mem. 9: 26, 55, 60, 81
SK 54	Juvenile calotte crushed	1949-50	Unpublished
SK 79	Early adult, anterior portion of crushed cranium w/ face and palate, post canine teeth	1949-50	Trans.Mus.Mem. 9: 60

Page 178 Line 4 correct spelling of chronostratigraphically.
Line 8 correct spelling of member.

Page 184 Line 3 change "Page 294" to "Page 303".

Page 185 Line 19 correct spelling of from.

Page 211 Line 5 correct spelling of above.

Page 214 Add as a note:

See Leakey, R. E. F. Nature 242: 170-173 attributes Lothagam specimen to genus *Ramapithecus* ? instead of *Australopithecus*.

Page 216 To Bibliography add:
Eckhardt, R. B.
1977 Hominid origins: The Lothagam problem. Current Anthrop. 18(2): 356

Page 223 Line 5, between Members and E add upper.
Add as final sentence to first paragrsph: "Likewise and equally important consideration is the apparent absence from the Koobi Fora region of fossiliferous sediments yielding faunas equivalent to those of the Shungura Members C-E. (Harris, 1977)
In Figure II-23, under Omo, Shungura Fm. change E to G and G to E; reading down zones are properly G, F. E, D, B.

Page 238 In Bibliography add:

Harris, J. M.
1977 Paleomagnetic stratigraphy of the Koobi Fora Formation east of Lake Turkana (Lake Rudolf), Kenya. Nature 268: 669-70.

Hillhouse, J., J. Ndombi, A. Cox and A. Brock
1977 Additional results on paleomagnetic stratigraphy of the Koobi Fora Formation, east of Lake Turkana (Lake Rudolf) Kenya. Nature 265: 411-15.

Page 268 Line 14, change (page 283) to (Page 292).

Page 279 After last sentence in second paragraph add: (Aronson *et al*, 1977).

Page 280 Line 25 correct spelling of auditory.

Page 286 Add: Additional References

Johanson, D., M. Taieb, B. Gray and Y. Coppens. In *Geological Background to Fossil Man*. ed. W. W. Bishop Geological Society, (In press)

Taieb, M., D. Johanson and Y. Coppens. 1975 C.R. Acad. Sci. 281D: 1297-1300.

Johanson, D., and Y. Coppens 1976 A.J.P.A. 45: 217-234.

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AUTHOR'S PREFACE

The study of "man's" origins from a scientific point of view is a relatively recent discipline when one considers history or philosophy or even medicine, whose basis for study goes back to the earliest written records. Yet "man" has always wondered about "man" and attempts have been made throughout our history to account for our "place in Nature." The documentation of these attempts can be found in T. D. McCown and K. A. R. Kennedy's Climbing Man's Family Tree. It is this most important background information which, when understood, makes a good deal more sense out of the enormous amount of data we have to work with today in the attempt to address ourselves to the questions of our earliest origins.

It took so much work, so much effort against enormous prejudice to arrive at that right point in time where these problems could be considered scientifically. It began with Darwin and others of his time, Wallace, Huxley and Mendel, to name only a few, and it has not ended nor is any end in sight. Bernard Campbell has recently written: "Paleoanthropology is becoming a real science at last, where analysis can precede hypothesis, and where progress takes the form of an orderly revision of the consensual working hypothesis. In this way, we move step by step up the ladder of induction to better understanding of man's place in Nature" (Campbell 1973: 200). Increasing numbers of scientists are turning their interests to the study of man's origin to such a degree that paleoanthropology has become the subject matter of biochemists, geologists, paleontologists, geochemists, botanists, zoologists, geneticists and anthropologists. It is one of a few fields whose members come from the widest range of scientific disciplines.

This Fourth edition is a reflection of the multidisciplinary approach to this study. It is an attempt to present as much of the published data as possible from a wide range of scientific endeavors. It could easily be larger for much of the important work of others has been trimmed and abstracted to the point, some may argue justifiably, that some aspects of the state of the art are not fairly presented. In this edition, however, we have made the attempt to represent most of the major contributions and have provided a bibliography for each section so that problems can be more clearly identified and investigated by the reader. We hope that the major contribution of this volume to the study of man is that it will be a valuable compendium of a wide variety of knowledge of other scholars presented by the authors, hopefully, without prejudice to a particular point of view. Its real value, however, is that it can be and will be periodically updated with the welcome assistance of all who read it.

We thank the National Science Foundation and the American Association for the Advancement of Science for providing the mechanism which allows this information to have as wide a distribution at minor cost.

The authors wish to thank Dr. A. Wilson who generously provided laboratory space and advice. Dr. V. M. Sarich also generously provided advice and guidance in the original research and study of the pertinent literature. Both of these individuals have been instrumental in contributing to the field of molecular evolution and to the growing field of molecular anthropology.

We thank Mr. Kenneth Miller and Melvin Clinton for their time in typing the manuscript and further owe a debt of gratitude to Ms. Linda Murdock in the preparation of many of the edition's figures. We also acknowledge with thanks Mr. Fraiser McConnell for his many hours in editing the final manuscript; George Shkurkin whose subtle contributions appear throughout; Professor Sherwood Washburn for his many inspirations before this project was ever envisioned, and T. D. McCown in whose memory this effort is dedicated.

A. INTRODUCTION

Why Study Macromolecules?

In order to fully understand how species differ from one another and how the various distinguishing characteristic features come to be, it is first necessary to place the species in a phylogenetic framework. Lacking this framework, it is impossible to expect to fully answer the how and why questions concerning the evolution of a species. In the pursuit of the how and why questions, evolutionary biologists draw from many sources of evidence, including information from studies of the comparative anatomy of living species, from behavioral information, from evidence from the fossil record, and most recently from evidence drawn from comparisons at the macromolecular or biochemical level. Each source of data has specific limitations and specific advantages, yet they may be used to complement one another in compiling a total evolutionary picture.

One of the most interesting, as well as the most controversial, issues, presently as well as historically, is the question regarding man's origin. What living form or forms is most closely related to man? What was the ancestral form like? Opinions merely regarding the temporal origin of man vary widely, ranging over a span of almost 30 million years. Kurten (1970) suggests man's lineage appeared approximately 30 million years ago in the early Oligocene, while Sarich and Wilson (Sarich and Wilson 1967b; Sarich, 1968) have suggested that man's lineage separated from that leading to the African apes, chimpanzee and gorilla not much more than 5 million years ago. Other individuals take something of an intermediate stance (Simons 1972; Leakey 1969).

One's view of man's evolution depends on the following considerations; 1) what form is seen as being ancestral, 2) what are the closest living relatives, and 3) what is the time of separation of these ancestral lineages. There are a number of controverises which can be traced simply to what perspective an individual assumes. For example, there is a controversy over what morphological pattern is antecedent to the development of the bipedal locomotion that characterizes modern men. That is what locomotor pattern characterized the ancestral proto-hominid? If man's lineage diverged from that leading to other hominoids in the earliest Oligocene, then the ancestral locomotor pattern was probably arboreal quadrapedalism such as is seen in modern Old World monkeys. If hominids originated in the early to mid-Miocene, 15-20 million years ago, then the ancestral locomotor pattern may have been incipient brachiation. An origin of the hominid lineage in the late Miocene-early Pliocene, 4-8 million years ago, suggests that the ancestral form had for some period of time passed through a well developed brachiating tage (though probably not as well developed as is seen in the modern gibbon), and that the subsequent proto-australopithecines may have even passed through a knuckle-walking phase (Tuttle 1974; Washburn 1971).

The lack of an adequate fossil record and the debate engendered over various proposed ancestral hominids such as Ramapithecus (Simons 1972; Simons and Pilbeam 1965; Pilbeam 1966; Walke Andrews 1973; Andrews 1974) or Kenyapithecus africanus (Leakey 1968b; Simons 1969) has forced students of human evolution to rely primarily upon comparative morphological and behavioral evidence. Similarities therefore seen between living and fossil forms may be due to shared ancestral characteristics. However, morphological similarities may be due to parallelisms or convergences rather than inheritance of traits from a common ancestor, and these similarities in grade may not be due to the derivation of such shared traits along an inferred ancestral-descendent lineage (Delson 1974).

What is needed is a source of information that allows unambiguous answers or conclusions to be drawn regarding phylogenetic or temporal relationships. Comparisons between the proteins or nucleic acids of living species provide just such a source of data. The development of these techniques of comparison of macromolecules, some tracing back to over seventy years (Nuttal 1902, 1904), has revolutionized the study of evolution. With the knowledge of the structure of DNA and the knowledge of the relationship of genes to polypeptide chains, relationships by assaying the nucleic acids or protiens of living forms.

Molecular evidence concerning the actual phylogenetic position of man vis a vis the other primates is now rapidily accumulating. The data suggests that man is closely related to the chimpanzee and gorilla - the great apes- and that the latter are not more closely related to each other than either is to man (Goodman 1961; Hafleigh and Williams 1966; Sarich and Wilson 1967b; Kohne 1970; King and Wilson 1975; Sarich 1968, 1971; Cronin 1975; Sarich and Cronin 1976) Man and chimpanzee are so close that they differ by only about 1-2% in their DNA sequence (Kohne 1970, Hoyer et al. 1972). This is an extremely close relationship, similar to the DNA differences seen between groups of baboons of the genera Papio and Theropithecus. Though the morphology of human and chimpanzee is quite distinct it is also quite apparent that there are many similarities, particularly in the thorax and upper limb areas. This was recognized over 100 years age. T. H. Huxley concluded, in 1863, that "every bone of a gorilla bears marks by which it might be distinguished from the corresponding bone of a man; and that in the present creation, at any rate, no intermediate link bridges over the gap between Homo and Troglodytes. It would be not less wrong than absurd to deny the existence of this chain; but it is at least equally wrong and absurd to exaggerate its magnitude, and, resting on the admitted fact of its existence, to refuse to inquire whether it is wide or narrow." We now know that this chasm is both narrow, at the genetic level, and relatively wide at the morphological level. This is borne out by the recent documentation of the independence in rates of morphological and molecular evolution in the evolution of species (King and Wilson 1975). The molecular data reflecting the clsoe genetic relationship, can be interpreted to suggest that humans and chimpanzees may have diverged approximately 5 million years ago (Sarich and Wilson 1967b; King and Wilson 1975; Sarich and Cronin 1976). From this conclusion it would follow that the ancestral morphotype of the common ancestor of the African apes and man may have resembled a modern day chimpanzee (Sarich 1968), or even more likely a pygmy chimpanzee (Pan paniscus). The method of locomotion employed by this common ancestor may have been a knuckle-walking form of terrestrial progression derived from an ancestor capable of full brachiation, i.e. that which is seen in living chimps. This is a hypothesis which Washburn has previously suggested based purely on morphological criteria (Washburn 1968). Natural selection presumably acted with rapidity in order to adapt the protohominids for efficient bipedalism, because by approximately 3 M.Y. ago Australopithecus was essentially fully bipedal (Zihlman 1970). In addition to being an aid in developing a protohominid model, the molecular data lead to implications for interpreting the fossil record. If a hominid lineage did not exist until 5 million years ago then, clearly, Ramapithecus cannot be a hominid. Thus, the use of comparative molecular data allows inferences to be drawn concerning morphological or fossil evidence, and in the case of human evolution allows a clear cut choice among extreme alternatives.

What is it about comparative protein and nucleic acid studies that makes them so potentially useful in solving evolutionary relationships? The answer is that these macromolecules possess two uniquely useful properties not characteristic of any other source of comparative information. The first is their ubiquity -- all primates have albumins, transferrins, hemoglobins, and DNA's of very similar, if not identical, function and basic structure. Secondly, the unit of evolutionary change involved in producing the differences seen among these molecules in different taxa -- amino acid or nucleotide substitution is known. Thus, it is possible to determine functionally equivalent or evolutionarily homologous entities between very diverse taxa simply by counting these substitutions. The problem, of course, lies in developing appropriate methods of counting and relevant models of interpreting the data so obtained.

The four basic methods, to be discussed below, are amino acid or nucleotide sequencing, nucleic acid hybridization, electrophoresis, and lastly, immunology; each with its own utility in providing quantitative macromolecular comparisons. The data such comparisons provide very in the ease of obtaining them, in the taxonomic levels at which they are useful, and in the fidelity with which they accurately reflect the actual substitutions which occurred along the lineages leading to the modern species being studied.

Using these techniques, the differences in either proteins or nucleic acids can be measured, and a distance matrix can be generated. Once this is done, there are methods by which the matrix can be converted into a phylogeny. A phylogeny has three basic components:
1) cladistics, the branching or diverging order of the lineages;
2) patristics, the evolutionary change occurring along a lineage such as the development of bipedalism or even the number of amino acids substituted in a particular protein along a branch of a cladogram; and
3) chronistics, the time of separation of the various lineages.
Calculating these times of divergences from the molecular data depends on the observation that molecules evolve at a statistically constant rate. This was first noticed by Zuckerkandl and Pauling (1962, 1965) and further developed by Sarich and Wilson (1967a, 1967b, 1973) among others. If a certain reference point (a calibration point) is chosen from the fossil record for two species whose genetic distance is known, then if the molecule evolved at a constant (non-deterministic) rate, the molecule can serve as an evolutionary clock. Thus, approximate times of divergence of species can be calculated where only a genetic distance is known.

Proteins have within them a history. Their amino acid sequence must have followed an evolutionary pathway that can be deduced; therefore, it should be possible to construct cladograms by counting the differences among the homologous molecules of various species. Secondly, if the amount of change can be correlated with absolute time, a time scale can be added to the cladistic framework. Each animal has within it its own evolutionary genealogy and with the proper skills it is possible to translate this encoded genetic information into a quantitative phylogeny.

Macromolecules in Systematics

Beginning with the pioneering work of Nuttall (1902, 1904) macromolecules have become an increasingly powerful source of data in probing evolutionary relationships. As knowledge of mechanisms of evolution grew and with the advent of better techniques, macromolecules became more and more useful. There are now four major basic techniques employed in ascertaining genetic relationships as revealed by macromolecular differences. All are useful, but are appropriate at different times to different questions or problems. As mentioned previously, the methods include 1) amino acid sequencing; 2) DNA hybridization, 3) electrophoresis, and 4) immunology.

Amino acid sequencing has now been used to determine the primary structure of many proteins. A few that have been useful in molecular systematics of mammals are: cytochrome C (Fitch and Margoliash 1967; Dickerson 1971, 1972), fibrinopeptides (Doolittle *et al*. 1971; Wooding *et al*. 1972), lysozymes (Prager and Wilson 1971a, 1971b), haemoglobin (Zuckerkandl, 1965; Air *et al*. 1971; Goodman *et al*. 1973, 1974; Matsuda *et al*. 1973a, 1973b, 1973c, and myoglobin (Air *et al*. 1971, Romero-Herrera *et al*. 1973, 1976). Once the sequences of a number of homologous proteins are known, one can construct a cladogram of the various lineages. Fitch and Margoliash (1967) have analyzed the sequences of over twenty cytochromes C from eukaryotic organisms and have developed a phylogeny for these organisms. Recently, both Fitch (1973a, 1973b) and Dayhoff (1969a, 1969b, 1972, 1973) have extended this cladogram as more sequences became available from various other taxa. Goodman et al. (1971, 1973, 1974) have generated extensive mammalian phylogenetic trees using haemoglobin sequences.

The technique is extremely useful, potentially surpassed only by base sequencing of the DNA itself for constructing phylogenetic trees, as such proteins only partially reflect DNA base sequence due to the degeneracy of the genetic code. There are a few drawbacks with this technique. It is extremely time consuming. A large molecule of 500 amino acids may take years to finish. It can be economically unsound with regards to material, and from certain species such as Daubentonia, it may be impossible to collect enough material to do a proper sequence. Given the present state of the technique, it is also impractical to consider using it to do an intensive systematic survey of a selected group.

The second and most recent method of determining genetic affinity of organisms is nucleic acid hybridization. This technique has been employed by Kohne (1970), Hoyer et al. (1972), Laird, McConaughy and McCarthy (1969) and Kohne et al. (1972). DNA, when sheared or fragmented and heated to an appropriate temperature, will separate into its two constituent chains. Upon subsequent cooling, the chains will reanneal or reassociate into their proper configuration with pairing occurring between opposite complementary strands. The degree to which heterologous DNA reanneals compared to the native or homologous DNA is a measure of the relatedness of the two sequences of DNA being compared. The differences may be measured as a Tm (change in thermal stability) and expressed in terms of a per-cent base pair mismatch. The greater the base pair mismatch the lower the melting point of the hybrid DNA molecule. Kohne *et al*. (1972) and Hoyer *et al*. (1972), have employed this method to construct cladograms of this single character measurement for the primates with particular reference given to hominoids.

Intrinsically, this method is extremely useful as one is supposedly viewing the entire genome of an organism. However, there is both a close and distant limit to what one may measure. The method is insensitive for interpopulation (deme) distances or even closely related species although it gives the indication one is looking at closely related organisms. The distant limit is within a mammalian order. For instance, the *Homo-Galago* relationship which is a comparison between suborders, is at or beyond the limit of the method. Obviously one could not attempt to do cross ordinal, class or even phylum comparisons such as have been done with various slowly evolving proteins. Extensive surveys of taxa are expensive in both time and material.

The third technique, electrophoresis, is currently the most popular method employed by evolutionary biologists. Proteins are placed in an electric field in a particular suspensory medium (starch or acrylamide). Proteins coded by a specific locus from different organisms may have different net charges and may be discriminated by differential migration in this medium. Since the original population genetics oriented work of Hubby and Lewontin (1966), the technique has proven useful in the study of genetic variability of populations including gene frequency analysis and individual heterozygosity The method in recent years has proved extremely popular, and it has been extended from measuring differences between populations to higher taxonomic categories. Various animals and plants have been surveyed electrophoretically including Drosophila (Ayala _et_ _al_., 1972a, 1972b), _Avena_ (Allard _et_ _al_. 1972; Clegg _et_ _al_.1972a, 1972b; Havrick and Allard 1972), Rodentia (Selander _et_ _al_. 1969, 1973; Johnson and Selander 1971), non-human primates (Weiss 1972; King 1974; King and Wilson 1975) and humans (Harris 1966; Nei 1971, 1972).

The method has its maximum utility at lower taxonomic levels. Eventually, all the proteins will have accumulated charge changes and a maximum differentiation will have been attained. Thus there is a genetic distance limitation to the method. One should survey many loci and should attempt to screen as many individuals as possible from the group or groups in question so that one maximizes the likelihood of viewing all the polymorphisms present. Once the raw data are generated, methods of converting them into distance measurements are available (Selander 1969; Nie, 1971, 1972). Nei's ideas are intriguing, for given certain assumptions concerning the rate of substitution of certain molecules and the proportions of mutations which lead to charge changes, one is able to convert distance measurements into a time scale. In any case, a relative scale is deduced from the raw data alone without the addition of a time dimension.

Beyond the genetic distance limitation, another drawback is that a large amount of variability is missed, for with a random distribution of mutations, only about one in four yields a charge change. Also, charge may be conserved evolutionarily as Sarich (1972) has demonstrated in detecting immunological differences among carnivore haemoglobins from different taxa that were electrophoretically identical, indicating that an overall net charge may remain constant as the primary sequence varies. As a technique, electrophoresis underestimates the amount of variability within a population.

The fourth general method useful in studying evolutionary relationships is immunology. Basically, antibodies are produced in a host animal to an antigen and then similar (homologous[1]) molecules are reacted with the antibodies and the amount of reaction is measured. The standard to which one needs to refer is the amount of reaction of the antibodies and the molecule that they are directed against. Antibodies recognize best the antigen against which they are directed, and recognize less well a homologous antigen that has changed somewhat -- e.g., the same protein in a related species. The greater the sequence difference, the less the recognition, until recognition is completely lost when there is 35 - 40% sequence difference Thus one has a general scale of difference and this has been recognized since the early twentieth century in Nuttall's work (1902, 1904). Williams (1964) has an excellent discussion of the uses of the immunological approach to protein evolution.

A standard immunological technique has been quantitative precipitation, where the amount of precipitation is measured when antibodies are complexed with antigen in large amounts. It is possible to measure relative differences from the homologous[2] antigen / antibody reaction when a specific antobody is reacted with a heterologous antigen. Nuttall observed that the degree to which the reaction lessened was correlated with taxonomic distance; Hafleigh and Williams (1966) made similar observations. Sarich (1972b) has employed this technique in his extensive surveys of marsupials, rodents, and carnivores. Weigle (1961) has reported on undulate albumins and Wang et al. (1968), using inhibition techniques, have studied primate transferrins.

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[1] Homologous in this sense means molecules that share ultimately a common ancestral gene.

[2] Homologous in this sense may be defined as the antigen against which the antisera is directed. Heterologous is any antigen other than the one against which the antisera is directed, although these heterologous antigens are homologues of the antigen to which the antisera is directed.

A second technique involves the observation of precipitation lines between antibody and antigen in an agar gel (Stollar 1963). The antibody and antigen are each placed in a seperate well cut in the gell. Diffusion occurs, and upon antibody recognition of an antigen, a precipitation line will form. Mohagheghpour and Leone (1969) and Bauer (1970, 1973) have employed this method in studies of primate proteins. Goodman (1961, 1962, 1963a, 1963b) and Goodman et al.(1971) have also employed this method in extensive studies of primate relationships.

The last immunological technique to be described is micro-complement fixation which was developed by Wasserman and Levine (1961). It involves measuring the amount of complement (a series of enzymes found in vertebrate serum; Mayer 1973) fixed or trapped in the antigen / antibody matrix while suspended in a buffer solution. Using antisera produced to a specific protein, the difference between the homologous and heterologous antigens can be measured with this technique.

The difference between the two antigens can be expressed as the degree to which the antibody concentration must be increased with the heterologous antigen as compared to the homologous antigen in order to fix equal amounts of complement in the antigen / antibody matrix. This measurement has been called the index of Dissimilarity (I.D.) (Wilson et al. 1964). The I.D. increases as genetic distance increases, and Prager and Wilson (1971a, 1971b) have shown a direct correlation between I.D. and the number of amino acids substituted in avian egg white lysozymes. Similar results have been obtained with azurin and oerredoxin (Champion et al. 1974). Various proteins have been used as antigens and now quite a few taxonomic groups have been investigated. These include: 1) serum albumin, perhaps the most widely employed molecule, in primates (Sarich 1967, 1968, 1970, 1971, 1972b; Sarich and Wilson 1966, 1967a, 1967b; Wilson and Sarich 1969; Cronin and Sarich 1975), carnivores (Sarich 1969a, 1969b, 1972a, 1973, 1974), in rodents, (Sarich 1972a; Keeler and Sarich unpub. obs.), in anurans (Wallace 1971; Wallace et al. 1971, 1972, 1973; Maxson 1973; Maxson and Wilson 1974, 1975:, in reptiles (Gorman et al. 1971; Wyles and Sarich unpub. obs.); 2) Lysozymes in birds (Prager and Wilson 1971a, 1971b), in primates (Hanke et al. 1973); 3) carbonic anhydrase in primates (Nonno et al. 1969); 4) lactate dehydrogenase in vertebrates (Wilson and Kaplan 1964; Gorman et al. 1971); 5) azurin in bacteria (Champion et al. 1975); 6) ferredoxin in bacteria

(Champion 1972; 7) alkaline phosphatase in bacteria (Cocks 1971; Cocks and Wilson 1969, 1972; for other micro-complement fixation studies of bacterial protein evolution see Steffen et al. 1972 and London and Kline 1973 for references), and 8) transferrins in primates (Cronin and Sarich 1972, 1973a, 1973b, 1974), in rodents (Sarich, unpub, obs.), in carnivores (Sarich 1973; Sarich, unpub. obs.), and in birds (Prager et al. 1974).

The last method described above, micro-complement fixation, has many advantages. It is sensitive, often being able to detect single amino acid substitutions (Cocks and Wilson 1969; Cronin 1975). It is economical, using only microgram quantities of material. Extensive surveys of many groups can be carried out in a relatively short period. The antigen need not be purified, as whole serum can be used as the heterologous antigen source (Sarich 1967). Also, the technique is capable of being employed over wide taxonomic distances such as within and between orders of mammals, among orders of birds, and within superfamilies of frogs and reptiles.

On the other hand micro-complement fixation does have a few limitations. The position of substitutions in the molecule cannot be known (as internal substitutions are not visible to the antibodies) and thus cannot be measured. However, a great majority of substitutions are external and thus visible (Dickerson 1971, 1972). Moreover, the sequence-immunology correlation is only approximate. Antibodies also fail to recognize as homologous those molecules which have evolved or changed approximately 40% or more of their sequence (Prager and Wilson 1971a, 1971b). Those molecules which evolve rapidly have a limited utility for determining genetic distances at higher taxonomic levels. In addition, there are problems of unknown dimensions. The first of these is the problem of changes in the structure of the molecule other than amino acid substitutions including deletions and partial duplications, etc., or differences in prosthetic groups such as carbohydrate side chains could arise. Secondly, conformational changes could occur during the course of the functioning of the molecule which might cover or expose antigenic determinants. Differences could also be due to post-translational modification as has been reported for mouse serum albumin (Wilcox 1973). The possibility exists that differences other than in the primatry sequence could produce immunologically detectable differences. The method, on the whole, is good for systematic work without being as time consuming as sequencing, or as complex as DNA hybridization: and is able to survey taxa at higher levels which are beyond the range of electrophoresis.

Evolutionary Clocks

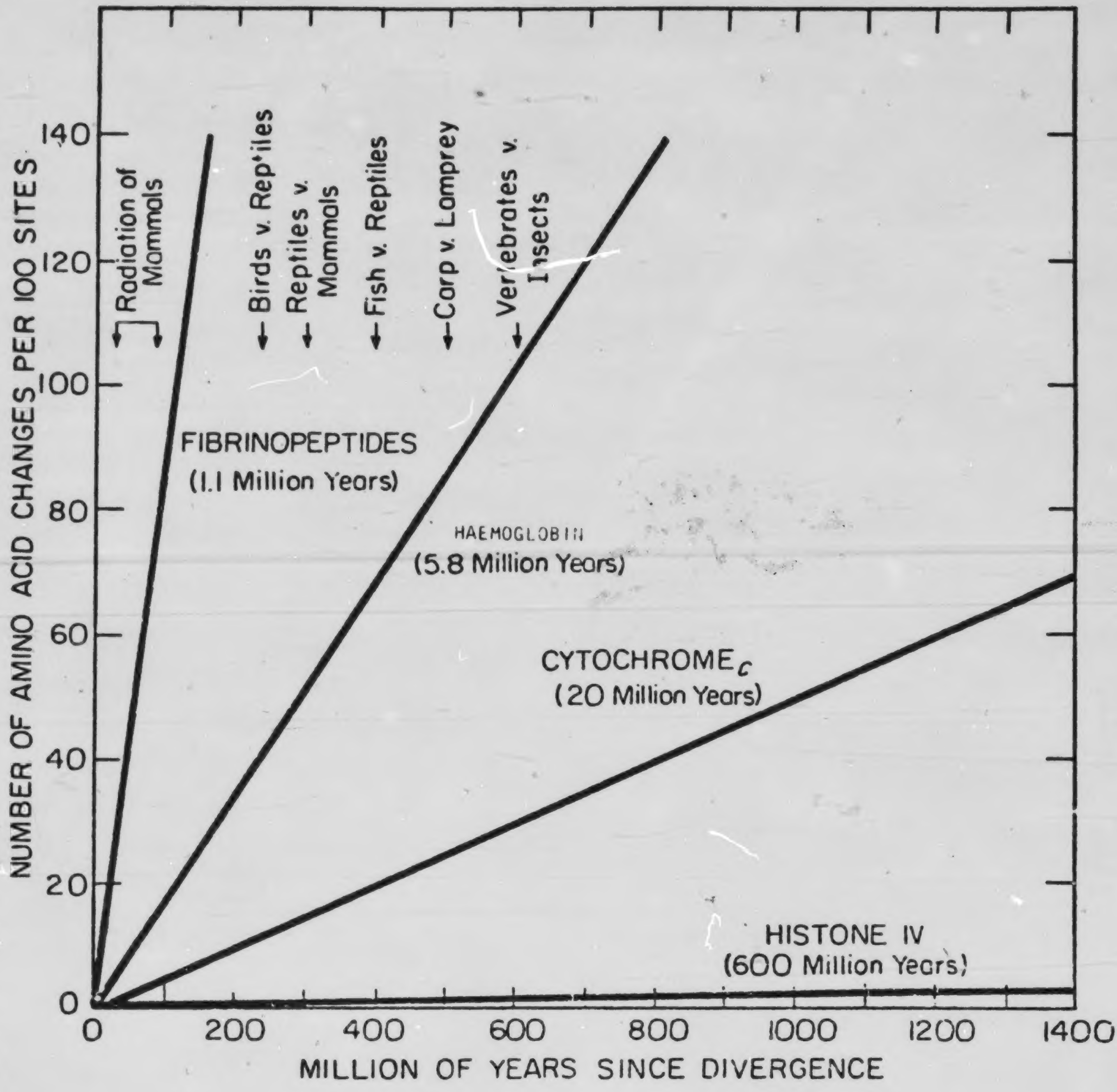
The idea that molecules might serve as evolutionary clocks was proposed by Zuckerkandl and Pauling in 1962, (see also Zuckerkandl 1965) based upon their investigation of Haemoglobin structure. This hypothesis was further strengthened by work done by Margoliash (1963), Smith and Margoliash (1965), Salthe and Kaplan (1966) and Sarich and Wilson (1967a, 1967b, 1973; Wilson and Sarich 1969). Sarich and Wilson observed that along different branches of a phylogeny there seemed to be about equal amounts of change, as measured by micro-complement fixation technique. This observation of regularity of protein evolution could be explained by describing evolutionary substitution occurring in a protein molecule as being stoichastic. That is, when the number and distribution of these evolutionary events were known, they would fit a Poisson distribution. Certain portions of the molecule could accept more changes and would tend to vary together (canvarions) (Fitch and Margoliash 1967; King and Jukes 1969).

Different molecules have different rates of evolution, and a standard has been defined as the Unit Evolutionary Period (U.E.P.). This is the time necessary for a one per cent (1%) change in sequence difference to develop between homologous macromolecules of two diverging lineages. The unit evolutionary period is 20 M.Y. (million years) for cytochrome C; 1.1 M.Y. for fibrinopeptides; and 6 M.Y. for histone IV, (Dickerson 1971, 1972; Dayhoff 1972) figure 1-1 For serum proteins the unit evolutionary period is fairly short. Albumin, based on sequence work (Brown unpub. obs.) and immunological data (Sarich 1967a, 1967b; Sarich and Wilson 1967a, 1967b; Wallace et al. 1971; Maxson and Wilson 1974) has a unit evolutionary period of about 2.5-3-0 M.Y. Serum transferrin has a unit evolutionary period of approximately 2 M.Y. (Mao and Dessauer 1971; Cronin and Sarich 1972, 1973).

Figure 1-1

Rates of evolution of proteins can be calculated by plotting average distance in amino acid sequences between species on two lineages whose divergence event can be dated. Divergence dates are drawn from the fossil record. Adapted from Dickerson (1972).

FIGURE 1-1


NUMBER OF AMINO ACID CHANGES PER 100 SITES
0
20
40
60
80
100
120
140
0
200
400
600
800
1000
1200
1400
MILLION OF YEARS SINCE DIVERGENCE
Radiation of Mammals
Birds v. Reptiles
Reptiles v. Mammals
Fish v. Reptiles
Carp v. Lamprey
Vertebrates v. Insects
FIBRINOPEPTIDES
(1.1 Million Years)
HAEMOGLOBIN
(5.8 Million Years)
CYTOCHROME C
(20 Million Years)
HISTONE IV
(600 Million Years)

Molecules have become widely used as molecular clocks in recent years and have been used to date the divergence times of vertebrates and invertebrates (Goodman et al. 1974), amphibians (Salthe and Kaplan 1966; Wallace et al. 1971, 1973; Maxson and Wilson 1974, 1975), reptiles (Gorman et al. 1971; Mao and Dessauer 1971), carnivores (Sarich 1969a, 1969b), Primates (Sarich 1966, 1968, 1970; Sarich and Wilson 1967a, 1967b; Wilson and Sarich 1969; Goodman et al. 1970), marsupials (Sarich unpub. obs.; Air et al. 1971) and micro-organisms (Cocks 1971; Champion 1972).

This observation of the seeming regularity (in a probabilistic sense) of protein evolution has caused extensive controversy, yet a plausible explanation has been offered. King and Jukes (1969), Kimura (1968, 1969), Kimura and Ohta (1971a, 1971b), Ohta (1972) and Lhta and Kimura (1971a, 1971b, 1971c) have hypothesized that some portion of the mutations occurring at the DNA level are neutral at the level of the protein (in terms of allele fitness) and that these new alleles can be incorporated into the population and fixed by genetic drift. Neutral substitutions are substitutions in the polypeptide chain in a position where more than one specific amino acid may be inserted without conferring either a selective advantage or disadvantage on the new allele. These calculations were originally based upon the supposed rate of mutation and the projected substitutional load. Various authors have criticized the concept of neutral mutation and have inferred that selection would indeed be operating upon every allele substitution (Smith 1968; Clarke 1970a, 1970b; Arnheim and Taylor 1969; Richmond 1970). Uzzell and Corbin (1971, 1972) have published an alternative distribution curve, postulating that a negative binomial instead of a Poisson has a better fit to the observed distribution of changes at the codon level. Specific criticisms suggest that not all lineages show an equal degree of evolution among them. Jukes and Holmquist (1972) noted a non-constancy of evolutionary rates of rattlesnake cytochrome C. Penny (1974), in taking specific issue with Jukes and Holmquist's observations, finds that rates along lineages vary greatly and thus pose a serious problem to the hypothesis of regularity of protein evolution. Langley and Fitch (1974) also see a large variation in rates of nucleotide substitution throughout vertebrate evolution.

In the specific case of primate evolution, a few authors questions regarding the regularity of rates of evolution for various molecules are as follows: Goodman (Goodman 1961, 1962, 1973a, 1973b; Goodman et al. 1971, 1973, 1974) is primarily responsible for postulating a placentation effect seen in the deceleration in the rate of protein evolution for those organisms with increased maternal fetal contact. Hoyer (Hoyer et al. 1972), Kohne (Kohne et al. 1972), and Lovejoy (Lovejoy et al. 1973) have all postulated a generation time effect with similar deceleration in the rate of protein evolution for those organisms with long generation times, in order to reconcile paleontological estimates of times of separation of taxa and the biochemical differences. This latter generation effect argument has been countered by Sarich (1972b) and Sarich and Wilson (1973).

B. MACROMOLECULAR DATA

The following section will present the molecular evidence concerning the phylogenetic relationhips within the primates with emphasis on man and his closest relatives, the apes, the taxonomic unit Hominoidea. There will be a brief explanation of each method coupled with the presentation of the raw "genetic distances" and a method of conversion of the data into a phylogenetic tree construction can be found in the references. The data will be organized by techniques and will be presented in the following order: electrophoresis, DNA hybridization, immunology, and lastly protein sequence.

1. Electrophoresis

Electrophoretic data that provides phylogenetic information within primates is relatively limited. There are a number of studies that detail polymorphisms in specific groups of primates, but these contain little comparative information for evolutionary purposes (Anderson and Giblett 1975; Barnicot and Cohen 1970; Barnicot and Hewett-Emmett 1971, 1972; Barnicot and Wade 1970). For a summary of human serum protein or red cell proteins polymorphisms, see Giblett (1969).

One key paper that does provide us with genetic distance and thereby phylogenetic information is the study by King and Wilson (1975). This paper details the average amino acid sequence difference between chimpanzee and man using electrophoretic criteria. The authors surveyed the electrophoretic mobility of 44 different structural genes of almost 100 chimpanzees. Of the 44 loci, 31 code for intracellular proteins and 13 code for secreted or extracellualr proteins. They subsequently compared the frequencies of the alleles at each locus with published reports of human allelic frequencies at the same loci.

Where the symbol represents the probability that human and chimpanzee will be electrophoretically identical at a particular locus i the equation is:

$$\delta_i = \sum_{j=1}^{A} X_{ij} \; Y_{ij}$$

Xij is the frequency of the jth allele at the ith locus in human populations and Yij is the frequency of the jth allele at the ith locus in chimpanzees.

The results show (Table 2, King and Wilson 1975) that about half of the proteins in the survey are electrophoretically identical for the two species and about half of them are different. A few loci are highly polymorphic in both species- The proportion of alleles at an average locus that are electrophoretically identical in human and chimpanzees populations is about 0.52. Furthermore, if it can be assumed that at a particular protein, amino acid substitutions have occurred independently and at random with respect to species since human and chimpanzee diverged then the number of proteins that have accumulated amino acid substitutions since the divergence approximates a Poisson distribution. Calculations from the data reveal that the average human protein is more than 99% identical in amino acid sequence to its chimpanzee homologue.

The actual human and chimpanzee genetic distance is about 0.62 using an index developed by Nei and Roychoudbury (1974). That is, there is an average of 0.62 electrophoretically detectable codon differences per locus between human and chimpanzee proteins. This degree of genetic distance is incredibly small given the major morphological and behavioral differences seen between humans and chimpanzees. This value corresponds to genetic distances found between sibling species of Drosophila or mammals. Nonsibling species, or congeneric species, differ more from each other by electrophoretic criteria than humans and chimpanzees. The human-chimpanzee distance does however, exceed populational differences found within species.

2. DNA Hybridization

There are relatively few studies using the techniques of nucleic acid hybridization that have relevance for understanding human or non-human primate evolution. The following data is drawn from Kohne (1970), Kohne *et al*. (1972), and Hoyer *et al*. (1972).

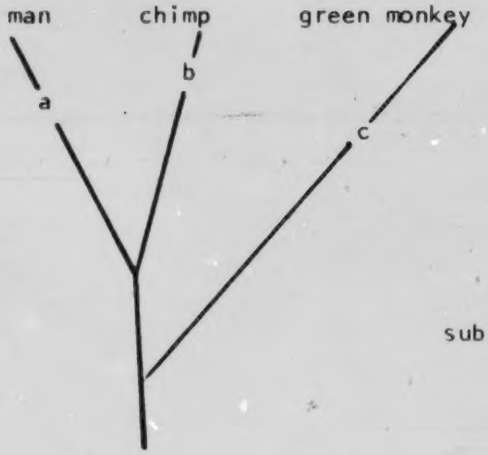
The procedure begins with the purification of DNA from an organi The purified native DNA, which exists as a long linear polymer of necleotide bases arranged in a double helix of paired complementing strands, can be readily spearated into two single strands by the use of heat. Given the proper conditions, the DNA will reassociate and reform a stable double strand DNA molecule almost, if not exactly, identical to the original native DNA. This ability to reform into the original structure is a consequence of the property of sequence recognition. This is a property that is extremely useful in comparing the genetic material of different organisms.

The actual mechanical procedure usually employs the use of a column of hydroxyapatite crystals. Under certain conditions hydroxyapatite will absorb double strand native or hybrid reassociated DNA. Single strand DNA (unhybridized into a duplex) will not be absorbed and will pass through the column. The double stranded DNA can be removed from the column by the use of heat which breaks the hydrogen bonds that hold the strands opposite each other. The thermal stability of the native double strand DNA can be measured and can be used as a standard to measure the degree of perfection of base pair matching between strands of DNA from differen organisms. The native DNA will disassociate into single strands at a specific repeatable temperature. The greater the difference between two organisms' DNA, the more imperfect the base pair matching in the hybrid duplex. Thus, there are less hydrogen bonds holding the complementary strands together. The less hydrogen bonding, the less energy in the form of heat is needed to disassociate the two strands (Table 1-1).

For example, the thermal stability of the native reassociated human-human duplex DNA is 82.6°C. The hybrid man-chimp duplex disassociates at 81.2°C, a difference of 1.4°C in thermal stability. Since man and chimpanzee last shared a common ancestor, the DNA sequences have diverged. The greater the phylogenetic distance between two species, the greater the mismatch in base pairing. The human-green monkey hybrid is 6.3°C less stable while the human-capuchin hybrid is 10°C less stable than the native human duplex (capuchin is a New World Monkey).

From a number of experiments using DNA's of known compositional differences, a standard has been calculated such that 1°C lowering of temperature in measuring thermal stability is caused by approximately a 1.5% difference in base pair sequence between two organisms DNA's. Thus, chimpanzee and human DNA differ by about 2.4%. Human and green monkey differ by about 9.5%. Human and capuchin differ by about 15.8% in their DNA sequence. Tables 1-2 and 1-3 present the data from Kohne _et_ _al_. (1972) and Hoyer _et_ _al_. (1972), respectively.

The raw data can be converted into a cladogram. By using a series of simultaneous equations, the branch lengths or the amount of DNA sequence change expressed as a percentage can be calculated. For example, man and chimp differ by 2.4%, man and green monkey by 9.6%, and chimp and green monkey by 9.6%. Let man, chimps and green monkey be a, b, and c respectively.



We know a+b = 2.4%, a+c = 9.6% and b+c = 9.6% by direct observation.

Thus -

1)	2)
a+b = 2.4	a+c = 9.6
b+c = 9.6	a-c =-7.2
subtract a-c =-7.2	add 2a = 2.4
	a = 1.2
	.: b = 1.2

Since man and chimp separated each as undergone about 1.2% base pair substitution. With this procedure most of the lineage lengths can be solved. Figure 1-6 presents the cladograms obtained from the data from Tables 1-2.

3. Immunological techniques

Immunodiffusion experiments.

Goodman has employed this technique in extensive studies of primate relationships (Goodman 1961, 1962, 1963a, 1963b. Goodman et al. 1971; Baba and Goodman 1975; Dene et al. 1975). Others have also used this method (Bauer 1970, 1973; Mohagheghpour and Leone 1969). A detailed account of the procedure may be found in Goodman and Moore (1971).

Briefly, the amount of similarity between two different macromolecules may be approximated using antisera prepared to one of the proteins. The procedure entails observation in agar gel of the intensity of precipitation of antigen and antibody and the extent of non shared antigenic distance reflected in spur size.

TABLE 1-2

Extent of Nucleotide sequence change (Kohne et al., 1972)

DNA's reacted	Thermal Stability T.S.) (°C)	T.S. (°C)	Percent nucleotide substitution since divergence
Man-Man	82.6	0	0
man-chimp	81.2	1.4	2.4
man-gibbon	79.1	3.5	5.3
man-green monkey	77.5	5.1	9.5
man-capuchin	72.1	10.5	15.8
man-galago	55.0	27.6	42
man-rat			
Green monkey (G.M.)-G.M.	84.4	0	0
G.M. - rhesus	82.4	2.0	3.0
G.M. - man	78.0	6.4	9.6
G.M. - chimp	78.4	6.0	9.6
G.M. - gibbon	78.3	6.1	9.6
G.M. - capuchin	73.4	11.0	16.5
G.M. - galago	56	28.1	42.0
Mouse - mouse	85.7	0	0
mouse-rat	67.7	18.0	27.0
cow-sheep	77.0	6.0	9.0
cow-pig	69.0	14.0	21.0

TABLE 1-3

Relative thermal stabilities of human and orang DNA sequence reassociated in the presence of primate DNA fragments.

Reference Species	Hybrid DNA*					
	Human	Chimpanzee	Gorilla	Orang	Gibbon	Green monkey
Human	0	0.7	1.4	2.9	2.7	5.7
Orang	1.9	1.8	2.3	0	2.4	4.3

*hybrid molecule is composed of 1 strand of the reference species and a strand of a heterologous species. The relative thermal stabilities of the hybrid molecule are expressed as degrees centigrade difference from the native DNA thermal stability.

Goodman has developed a scale to quantify the degree of difference. Using multiple comparisons and set theory logic (Moore and Goodman 1968) a computer program translates spur size and intensity into a table of antigenic distances between two species. The results obtained from many comparisons are briefly summarized in Table 1-4. Results from Wang *et al*. (1968) are presented in Table 1-5. Table 1-6 summarizes results from Mohagheghpour and Leone (1969). These data are in close agreement with results obtained from other immunological techniques (Cronin 1975; Cronin and Sarich 1975; Sarich and Cronin 1976).

Quantitative Precipitation

This technique involves measuring the amount of precipitation that occurs when antibodies are complexed with antigen in large amounts. The actual procedure is detailed in Hafleigh and Williams (1966). In addition, immunological distance units, to be defined below, are interconvertible with percent reaction in quantitative precipitation (where the amount of homologous precipitation serves as the standard of 100%) such that 200 minus twice the percent cross reaction equals immunological distance (Prager and Wilson 1971a, 1971b). The following tables are drawn from Mohagheghpour and Leone (1969), Table 1-6, and Hafleigh and Williams (1966), Table 1-8.

TABLE 1-4

A summary of antigenic distances taken from Goodman and Lasker (1974). Genera have been grouped starting with the smallest antigenic distances and then going to more inclusive groupings.

		Average Antigenic Distance
Homo	vs. *Pan*, *Gorilla*	0.80
Homo, *Pan*, *Gorilla*	vs. *Pongo*	1.60
Homo, *Pan*, *Gorilla*, *Pongo*	vs. Hylobatinae	2.23
Hominoidea	vs. Cercopithecoidea	3.47
Catarrhini	vs. Platyrrhini	6.49
Anthropoidea	vs. *Tarsius*	9.16
Haplorrhini	vs. Strepsirhini	10.80
Haplorrhini, Strepsirhini	vs. Tupaiaoidea	11.46
Primates	vs. Other Eutheria	12.11-14.91
Eutheria	vs. Marsupiala	15.83

TABLE 1-5

Percentage cross reactivity of several nonhuman primate proteins compared with the corresponding human proteins (Wang *et al*. 1968).

SPECIES	Tf	M	gG	gA	gM	K	L
Homo sapiens	100	100	100	100	100	100	100
Pan troglodytes	100	98	90	100	90	100	76
Gorilla gorilla	100	100	91	100	28	100	89
Pongo pygmaeus	90	100	78	100	29	95	70
Hylobates sp.	90	81	60	99	6	87	70
Macaca nigra	64	96	97	100	72	75	37
Macaca radiata	71	97	-	89	63	89	36
Macaca nemestrina	74	97	88	93	78	79	41
Macaca speciosa	65	99	87	96	81	77	37
Macaca mulatta	70	71	95	92	50	64	36
Papio sp.	69	96	99	95	76	79	40
Cercopithecus aethiops	51	79	82	89	46	61	41
Cercocebus fuliginosus	73	96	95	93	79	81	39
Erythrocebus patas	71	82	93	85	43	66	45
Callicebus sp.	22	20					
Cebus capucinus	46	29					
Saimiri sciurea	40	22					
Aotus trivigatus	29	22					
Lagothrix sp.	31	64					
Saguinus oedipus	26	23					
Lemur fulvus	11	66	82				

TABLE 1-5 (continued)

SPECIES	Tf	M	gG	gA	gM	K	L
Nycticebus coucang	11	17	70	94	9	22	9
Galago senegalensis	4	4	20	82	12	23	12

Tf = anti transferrin, M = anti alpha 2 macroglobulin

gG = anti gamma G globulin, gA = anti gamma A globulin,

gM = anti gamma M globulin, K = anti Kappa chain,

L = anti lambda chain.

TABLE I-6

Immunological correspondence of Primates as determined by densitometric measurement of immunodiffusion tests and by using antisera against proteins from human serum. (Mohagheghpour and Leone 1969).

	Antisera							
Genus	A	G	H	C	gM	gG	T	Gc
Homo	100	100	100	100	100	100	100	100
Pan	94	62	70	89	74	71	80	87
Hylobates	83	59	64	80	58	53	74	70
Presbytis	81	38	45	54	56	50	56	54
Macaca	75	45	37	70	57	46	53	54
Cercopithecus	74	41	42	73	56	41	63	55
Theropithecus	76	28	40	74	56	47	52	58
Ateles	57	24	40	12	48	0	46	45
Saimiri	56	0	33	26	32	0	48	36
Cebus	63	0	33	27	23	0	42	40
Galago	48	0	28	9	21	0	0	0
Nycticebus	47	0	21	5	22	0	0	0
Tupaia	43	0	20	0	0	0	0	28

A = anti albumin, g = anti immune globulin, H = anti Haptoglobin 2-1, c = anti ceruloplasmin, gM = anti gamma M globulin, gG = anti gamma G globulin, T = anti transferrin, Gc = anti group specific component.

TABLE 1-7

Immunological correspondence of Primates as determined by turbidimetric precipitin tests and by using antisera against proteins from human serum (Mohagheghpour and Leone 1969).

Genus	Ceruloplasmin	Haptoglobin 2-1	Albumin		Globulin	
	W.C.A.	W.C.A.	W.C.A.	OP[2]	W.C.A.	OP
Homo	100	100	100	100	100	100
pan	45	58	90	97	78	84
Hylobates	34	47	77	90	58	67
Presbytis	28	39	73	83	51	65
Macaca	22	32	67	80	47	49
Cercopithecus	29	52	60	72	45	55
Theropithecus	24	38	63	73	43	53
Ateles	20	37	53	63	17	15
Saimiri	18	36	63	68	20	16
Cebus	15	17	52	60	23	20
Galago	14	26	48	51	15	12
Nycticebus	13	23	39	44	12	10
Tupaia	11	14	31	41	3	3

1- Whole curve area (W.C.A.)

2- Optimal proportions zone (O.P.)

TABLE 1-8

Immunochemical correspondence values of primate serum albumins based on quantitative precipitation techniques. (Hafleigh and Williams 1966).

	% cross section
Homo sapiens	100
Gorilla gorilla	92
Pan troglodytes	97
Hylobates lar	79
Macaca mulatta	82
Colobus polylkomos	78
Papio doguera	75
Cercocebus galeritus	79
Erythrocebus patas	76
Cercopithecus aethiops	79
Aotus trivirgatus	74
Ateles paniscus	58
Saimiri sciurea	60
Tamarin tamarin	54
Lagothrix lagotricha	61
Cebus apella	45
Lemur fulvus collaris	37
Lemur macaco	34
Lemur fulvus fulvus	37
Tupaia glis	31
Perodicticus potto	31
Galago cassicaudatus	28
Propithecus verraurixi	22

Micro-complement Fixation

Micro-complement fixation (MC'F) is an immunological procedure designed to measure the degree of difference between the same macromolecule from two different species. This degree of difference between two macromolecules is usually expressed in immunological distance units (I.D.). But, the actual differences are in terms of amino acid sequence differences. The exact amount of amino acid differences between two molecules is unknown in every specific comparison. However, it is thought that one I.D. unit is roughly equivalent to one amino acid difference in either albumin or transferrin, and the general agreement between I.D. units as measured by MC'F and percent sequence difference is quite good. Prager (Prager and Wilson 1971a,1971b) has shown a direct relationship between percent sequence difference and the immunological distance as measured by micro-complement fixation the relationship being $y = 5x$ where y = distance expressed as micro-complement fixation untis and x = percent sequence difference. Immunological distance (I.D.) can be defined as 100 log I.D. I.D. is the index of dissimilarity (Wilson et al. 1964; Sarich 1968). This is defined as the degree to which the antiserum concentration must be increased when reacted with the heterologous antigen to give the same amount of complement fixed as the homologous antigen with the antiserum. The equation for determining this distance measurement is:

$$\log \text{I.D.} = \frac{YH - yh}{m} + \log \frac{xH}{xh}$$

Where m = slope; YH = %c fixed at the peak of the homologous curve; yh = %c fixed at peak height in the heterologous curve; xH = antiserum concentration for homologous curve; and xh = antiserum concentration in the heterologous curve (Champion et al. 1974).

FIGURE 1-2

Analysis of Micro-complement fixation results using antisera to purified transferrins from Pan troglodytes reacted with the purified transferrins from Homo sapiens, Theropithecus gelada and Aotus trivirgatus. Experiments were performed at the appropriate antiserum concentrations to give equivalent percent complement fixation.

Anti *Pan Troglodytes* T_f Antiserum

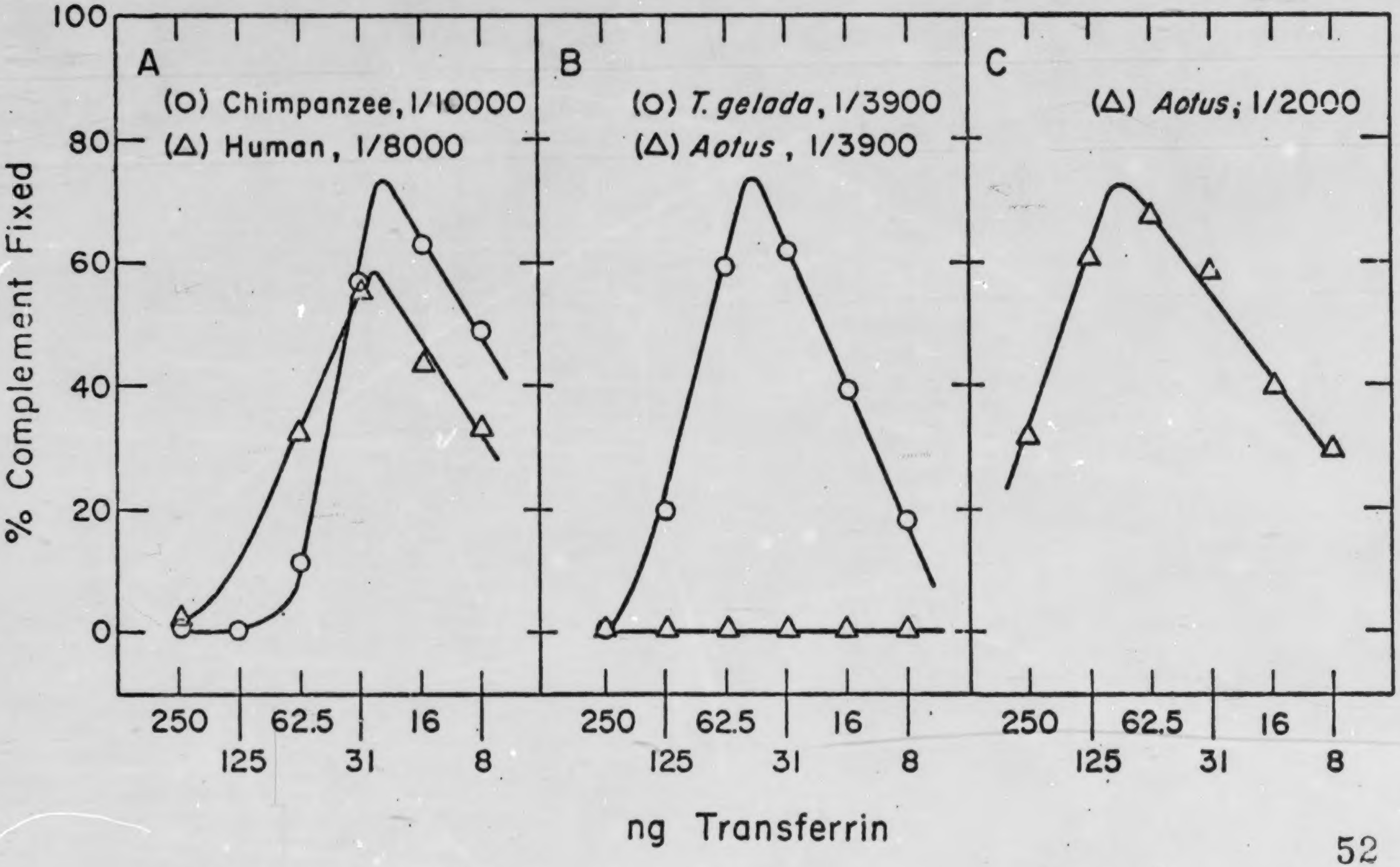


Figure 1-2

It is a property of the complement fixation system that after a certain amount of molecular difference accumulates between the homologous molecule and the heterologous molecule, the antiserum concentrations must be increased in order to give equivalent amounts of fixation. For example, anti *Pan troglodytes* Tf has a titer of 1/10,000. That is, 75% of the complement in solution is fixed when anti-*Pan* Tf is reacted with either *Pan* serum or purified transferrin at this antiserum concentration. If *Homo sapiens* Tf is reacted with this antiserum at a concentration of 1/10,000 a peak of only 40% complement fixation is attained. This suggests that changes have accumulated along both the human and chimpanzee lineage, or that since both last shared a common ancestor, one has changed relative to the other. It is necessary to increase the antiserum concentration to 1/7400 to reach 75% fixation giving an index of 1.35 or an immunological distance of 13. If transferrins from *Theropithecus gelada* and *Aotus trivirgatus* are reacted with the anti-*Pan* antisera there is no fixation at 1/10,0000. One has to raise the concentrations to 1/3880 (ID - 2.58) for *T. gelada* and to 1/1940 (ID = 5.15) for *Aotus* to reach 75% fixation. These correspond to immunological distances of 41 and 71 (Figure 1-2).

Quite a few studies using the MC'F technique have been employed in the study of primate relationships. These include 1) serum albumin (Sarich 1967, 1968, 1970, 1971, 1972b; Sarich and Wilson L966, 1967a, 1967b; Wilson and Sarich 1969; Cronin and Sarich 1975); 2) transferrin (Cronin and Sarich 1972, 1973a, 1973b, 1974, 1975; Sarich and Cronin 1976); 3) carbonic anhydrase (Nonno *et al*. 1969); 4) lysozyme (Hanke *et al*. 1973), Tables 1-9, 1-10, 1-11 are taken from Cronin 1975). Table 1-12 is from Nonno *et al*. (1969), and Table 1-13 is from Hanke *et al*. (1973).

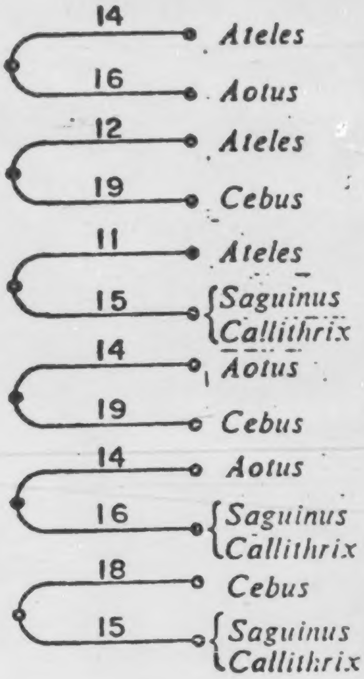
FIGURE 1-3.

A cladistic analysis conducted with the immunological distances between the transferrins of several platyrrhine monkeys. The immunological distance matrix is given at the top left. Within the matrix, the input data is given below the diagonal. The output data, calculated from the final cladogram (lower left), is given above the diagonal. At the right of the matrix is the mean immunological distance to these platyrrhine taxa from eleven catarrhine reference points. On the right, the intra platyrrhine distances are apportioned between every possible pair of taxa by the use of the eleven catarrhine reference points. The method of calculation is described in the text. The composite cladogram at the lower left is constructed from information of the lineage pair comparisosns at the right. The detailed explanation of cladogram construction is found in the text.

FIGURE 1-3

PLATYRRHINE TRANSFERRIN ANALYSIS

	At	*Ao*	*Ce*	*Sag* *Cal*	Catarrhini
Ateles	0	29	31	28	78
Aotus	30	0	32	29	80
Cebus	31	31	0	31	86
Saguinus *Callithrix*	26	30	33	0	83


14
Ateles
16
Aotus
12
Ateles
19
Cebus
11
Ateles
15
Saguinus
Callithrix
14
Aotus
19
Cebus
14
Aotus
16
Saguinus
Callithrix
18
Cebus
15
Saguinus
Callithrix

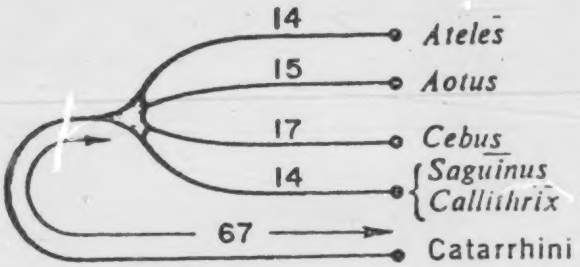

14
Ateles
15
Aotus
17
Cebus
14
Saguinus
Callithrix
67
Catarrhini

TABLE I-9

Immunological Distances Among Primate Albumins and Transferrins[a]

	H	C	P	Ta	Tu	Cy	Le	Lo	Non-primates[b]
Hominoidea	0	33	58	123	98	117	112	94	+19
Cercopithecoidea	45	0	56	128	102	114	110	107	+19
Platyrrhini	76	91	0	109	89	98	112	107	+12
Tarsius	172	164	156	0	93	109	122	95	+ 5
Tupaia	170	190	180	159	0	103	117	108	- 5
Cynocephalus	175	156	177	161	183	0	109	113	+ 5
Lemuriformes	164	171	164	156	178	162	0	88	0
Lorisiformes	196	195	193	178	183	185	118	0	-4

ALBUMIN

TRANSFERRIN

---

[a] These data have been gathered using antisera to the albumins and transferrins of *Homo*, *Pan*, *Gorilla*, *Pongo*, *Hylobates*, *Papio*, *Cercocebus*, *Cercopithecus*, *Presbytis*, *Aotus*, *Ateles*, *Cebus*, *Callithrix*, *Saguinus*, *Lemur*, *Avahi*, *Lepilemur*, *Propithecus*, *Phaner*, *Daubentonia*, *Nycticebus*, *Galago*, *Tupaia*, and *Cynocephalus*; to the transferrin of *Macaca nigra*; and to the albumins of *Ursus*, *Genetta*, *Hyaena*, *Felis*, *Hipposideros*, *Pteropus*, *Tadarida*, *Antrozous*, *Bradypus*, *Cabassous*, *Tamandua*, *Scapanus*, and *Solenodon*.

[b] These numbers represent the amount by which those albumins are more (+) or less (-) distant from the various nonprimates than the lemuriform mean. A similar analysis is not possible for the transferrins as antisera to nonprimate transferrins do not generally react with those of the primates.

TABLE 1-10

Immunological Distances Among Anthropoid Transferrins[a]

	HOMO	PAN	GORILLA	PONGO	HYLOBATES	PRESBYTIS	THEROPITHECUS	PAPIO	CYNOPITHECUS	ERYTHROCEBUS	CERCOCEBUS	ATELES	AOTUS	CEBUS	CALLITHRIX	SAGUINUS
Homo	-	13	5	33	27	64	55	61	49	52	42	73	73	75	70	86
Pan	7	-	5	36	27	54	52	56	46	46	41	71	73	74	70	74
Gorilla	8	10	-	37	26	59	50	52	45	49	39	75	73	62	68	76
Pongo	16	18	24	-	28	52	50	50	42	47	38	85	83	71	74	88
Hylobates	20	22	23	35	-	55	47	45	44	45	58	78	78	82	74	85
Presbytis	34	33	37	43	43	-	20	15	19	21	21	79	89	96	90	104
Theropithecus	41	41	51	66	53	43	-	3	20	24	24	100	100	112	103	113
Papio	37	36	37	61	45	34	5	-	18	21	23	98	100	109	101	110
Cynopithecus	34	33	31	44	39	34	13	16	-	12	12	86	89	100	85	101
Erythrocebus	34	33	31	40	37	34	16	20	19	-	23	86	86	91	81	94
Cercocebus	35	28	36	39	42	31	13	20	7	9	-	82	94	89	75	92
Ateles	64	78	61	83	84	95	85	68	82	75	79	-	28	30	26	25
Aotus	67	71	60	82	80	92	89	110	77	79	81	31	-	32	35	28
Cebus	66	83	70	101	86	90	95	108	72	81	79	32	30	-	36	32
Callithrix	67	82	70	92	89	97	85	99	71	76	81	28	30	29	-	8
Saguinus	64	80	68	95	87	97	92	106	78	75	81	28	30	35	6	-

[a] Antisera are directed against those purified anthropoid transferrins listed in Table 1.

TABLE 1-11

Immunological Distances Among Catarrhine Albumins.

ANTISERA

	HOMO	PAN	GORILLA	PONGO	HYLOBATES	M. IRUS	C. AETHIOPS	PRESBYTIS	C. GALERITUS	P. PAPIO
Homo	-	4	4	11	10	37	49	42	37	34
Pan	7	-	9	11	14	37	49	46	38	31
Gorilla	5	7	-	11	10	32	62	51	37	36
Pongo	12	8	10	-	11	42	57	48	38	40
Hylobates	13	13	12	11	-	36	49	44	35	43
M. irus	37	30	21	38	36	-	12	24	6	0
C. aethiops	44	42	21	33	37	10	-	22	9	4
Presbytis	42	40	22	38	38	24	34	-	28	16
C. galeritus	39	32	20	33	33	7	0	19	-	4
P. papio	40	30	18	34	36	2	7	25	8	-

TABLE 1-12

Immunological distance units among primate carbonic anhydrases, antisera prepared against carbonic anhydrase purified from *Homo sapiens*.

Species	*Immunological Distance*
Homo sapiens	0
Pan troglodytes	4
Macaca irus	51
Macaca speciosa	52
Macaca mulatta	53
Macaca cyclopis	56
Papio papio	62
Saimiri sciurea	81
Lagothrix lagotrichia	83
Cebus capucinus	89
Tupaia glis	115
Perodicticus potto	146

TABLE 1-13

Immunological differences among primate lysozymes

SPECIES	I.D. distance from human lysozyme	I.D. distance from baboon lysozyme
Homo sapiens	0	66
Pan troglodytes	0	67
Pongo pygmaeus	1	76
Gorilla gorilla	32	38
Cercopithecus aethiops	93	6
Cercopithecus talapoin	114	3
Macaca mulatta	122	1
Macaca speciosa	122	2
Papio cynocephalus	127	0
Macaca fasicularis	130	2
Macaca radiata	131	2
Saimiri sciurea	127	36
Saguinus oedipus	134	37
Callithrix jaccus	137	36
Lemur catta	151	203
Galago crassicaudatus	175	247
Lemur macaco	202	239
Lemur fulvus	212	235

For more data on specific taxa, refer to the papers detailed above, as the data presented is merely a representative sample of the available immunological data gathered using the MC'F technique.

Several objective methods of constructing phylogenetic trees from results of protein comparisons have been published (Fitch and Margoliash 1967; Sarich and Wilson 1967; Sarich, 1969a; Dayoff 1972; Farris 1972). These methods give rather similar results (Farris 1972; Wallace *et al.* 1973; Maxson and Wilson 1975). The method used in this study is outlined below (Cronin and Sarich 1975).

One begins the procedure by using the reciprocal immunological distances from an antisera matrix (a specific example is shown in Figure 1-3.) There are five antisera directed against the purified transferrins of New World monkeys *Aotus*, *Ateles*, *Cebus*, *Callithrix* and *Saguinus*. The averaged immunological distance between two forms are apportioned along the two lineages by using data provided by measurements made from outside reference points. The outside reference points in this case are 11 anti-catarrhine antisera (Table 1-10). For example, the *Aotus*-*Ateles* distance is 30 units, the average catarrhine-*Aotus* distance is 80 units, and the average catarrhine-*Ateles* distance is 78 units. The thirty units separating the transferrins of *Ateles* and *Aotus* should then be apportioned so that there are two more units along the *Aotus* lineage; i.e., a form further from the reference species has changed more. This procedure is repeated for every pair of taxa.

The next step is to compare one lineage, *a*, against every other lineage, and then group *a* with the lineage from which *a* has the smallest distance. In this case, Sanguinus and Callithrix are the closest pair:

they differ by 7 units; from any other New World monkey to either is an average of 30 units. *Sanguinus* and *Callithrix* can be treated as a subset or a cluster. A cluster exists when from the node that unites the taxa in question, the immunological distances that separate any taxa within the subset are less than the distance from any other form. The immunological distances from the forms involved in the cluster to every other form are averaged. This subset can then be treated as a single lineage *a*'; and tested sequentially with every other remaining lineage and joined with that lineage (i.e.,*c*) to which the distance is the least.

For example, suppose *a* and *b* differ by 8 units while *a* and *b* each differ by 16 from *c*, and there is no difference in rates as measured from the outside reference points. There are three pairs of taxa compared. Four units are separating *a* and *b* on each lineage. Similarly, along the lineages separating *a* and *c* and b and *c* there 8 units. The pair *a* and *b* are the closest and can be treated as a subset relative to *c*. The single lineage composed of *a* and *b*, *a*', has a length which is the average of the lengths as determined by the outside reference points in the *a* versus *c* and *b* versus *c* comparison. The *c* lineage is the average of the two comparisons of *a* versus *c* and *b* versus *c* also. The lineage length that unites *a* and *b* before their divergence into their separate lineages can be calculated by subtracting the averaged *a* and *b* lineage length separating the two as determined from the outside reference points, 4 units, from the total *a*' lineage length. The total *a*' lineage is 8 units, and thus the common lineage is 4 units long. The *c* lineage is 8 units. The addition of the remaining lineages proceeds in a stepwise fashion with *a*, *b*, and *c* (*a*' and *c*) treated as a single averaged lineage a'. This new composite lineage is tested against every other lineage until all lineages are placed relative to one another.

In Figure 1-3, Sanguinus and Callithrix represent a and b. Their average lineage length from their divergence is 4 units, while their common lineage a' is 14. That portion of the lineage which occurs after the divergence of any other form to the divergence of Sanguinus and Callithrix is thus 10 units.

In practice, the analysis is usually simplified as subsets are sometimes immediately apparent in the data. When this is observed, the distances to other forms from forms within the subset are averaged, and the subset becomes a single lineage. For example, there are 15 antisera to cercopithecoid transferrins (Cronin 1975). There are thus 15 separate lineages. However, they form readily definable subsets, and the 15 independent lineages can be collapsed into six composite lineages. This process of collapsing the data into readily apparent major lineages precedes the cladistic analysis detailed above. Upon subsequent analysis, the subsets can ve broken up into their own clade.

4. Protein sequences

Techniques exist that allow the specific sequence of amino acids in a polypeptide chain to be determined. Some data is now available for primates. These include fibrinopeptides (Doolittle et al. 1971; Wooding et al. 1972); haemoglobins (Matsuda et al. 1973a, 1973b, 1973c; Goodman et al. 1973, 1974; Boyer et al. 1971; DeJong 1971a, 1971b), and myoglobin (Romero-Herrera et ai. 1973, 1974). For brief summary of the protein sequence data available from primates see Goodman and Lasker (1973).

A number of different techniques for conversion of the protein sequence data into a phylogenetic tree have been published. (Fitch and Margoliash 1967; Dayhoff 1972; Farris 1972; Goodman _et al_. 1971, 1973, 1974; Goodman 1973). All give somewhat similar results.

Fitch and Margoliash (1967) have presented an elegantly simple method. First, a matrix of amino acid differences is tabulated for all species pairs. Abritrarily the closest two species, say _a_ and _b_, are chosen as the starting point for tree construction. These two species are considered a subset and the distances, in terms of amino acid differences, are averaged to every other species. The two subset lineages are aligned through use of the average distances of _a_ to every other species and _b_ to every other species such as is detailed in the DNA tree construction section. Similar simultaneous equations are established and using these average distances, lineage lengths a and b can be determined. The next closest lineage is added by similar methods until all lineages are added to the tree Arbitrarily, the next closest species pair is chosen, and the whole process begins again. This is repeated a number of times, and the best tree is chosen. The best tree is defined as the one where the percentage standard deviation is lowest. This is where the output data, the distances as calculated along the branches of the constructed cladogram, deviate least from the actual measured input data. Fitch and Margoliash originally employed this method in constructing a cladogram of sequences from 20 cytochrome c's. Recently Goodman (Goodman _et al_. 1971, 1973, 1974) has developed a more refined measure of converting amino acid sequence difference to minimum mutational distance (MM)) for each pair of sequences.

The calculation employs a conversion table based on the genetic code to determine at each position the minimum number of nucleotides that would need to be replaced or changed in order to convert a codon for one amino acid into a codon for another.

A computer program has been developed comparing both sequences of living species and sequences of constructed ancestral sequences of common ancestors at tree nodes. The best estimation of the correct phylogeny is the tree which overall has the minimum number of mutations. This method has been called by Goodman "the maximum parsimony method." The procedure seeks that tree of the amino acid sequences of living species with the maximum number of codon identities due to inheritance from common ancestors. Goodman feels that such trees are theoretically best because it seems more probable that the identities in codon sequences are due to common inheritance. The program selects the solution which minimizes the number of times a mutation is counted among lineages between the most ancestral point on the tree and each contemporary species. The mutational distance between any two species along the branches is the maximum parsimony distance (MPD). For a detailed account of this procedure see Goodman _et al_. (1973, 1974).

The following tables present the actual amino acid differences found for specific sequence comparisons. Table 1-14 is from Wooding and Doolittle (1972). Table 1-15, and 1-16 are from Goodman and Lasker (1973). Table 1-17 is from Romero-Herrera _et al_. (1973, 1974).

TABLE 1-14

Minimum numbers of amino acid replacements and base substitutions separating fibrinopeptides A and B of twelve primates (Wooding and Doolittle 1972). Amino acid differences are below the diagonal and minimum base substitutions are above the diagonal.

	Slow loris	Cebus	Spider	Drill	Green	Rhesus	Gibbon	Siamang	Orang	Gorilla	Chimpanzee	Human
Slow loris	-	17	17	21	18	20	16	16	17	19	19	19
Cebus monkey	15	-	3	11	8	11	8	7	8	10	10	10
Spider monkey	15	3	-	13	10	13	8	8	9	10	10	10
Drill	21	11	12	-	3	6	7	5	6	8	8	8
Green monkey	18	8	9	3	-	3	4	2	3	5	5	5
Rhesus monkey	19	11	11	6	3	-	6	5	6	6	6	6
Gibbon	16	8	8	7	4	6	-	2	3	5	5	5
Siamang	16	7	7	5	2	5	2	-	1	3	3	3
Orang	17	8	8	6	3	6	3	1	-	2	2	2
Gorilla	18	10	9	8	5	5	5	3	2	-	0	0
Chimpanzee	18	10	9	8	5	5	5	3	2	0	-	0
Human	18	10	9	8	5	5	5	3	2	0	0	-

TABLE 1-15

Amino acid differences of haemoglobin alpha chains within primates. (Goodman and Lasker 1973).

	Man	Chimp	Gorilla	Lan	Mac	Gal	Slow	Lem	Sif	Tree
Man	0									
Chimpanzee	0	0								
Gorilla	1	1	0							
Langur	3	3	4	0						
Macaque	4	4	5	5	0					
Galago	13	13	12	13	12	0				
Slow loris	9	9	8	10	11	8	0			
Lemur	15	15	16	15	16	16	14	0		
Sifaka	19	19	20	20	19	21	19	13	0	
Tree shrew	24	24	25	24	21	24	22	25	26	0

TABLE 1-16

Amino acid differences of haemoglobin beta chains within primates (Goodman and Lasker 1973).

	Man	Chimp	Gor	Gib	Lan	Mac	Mar	Nig	Spl	Squ	Slo
Man	0										
Chimpanzee	0	0									
Gorilla	1	1	0								
Gibbon	3	3	4	0							
Langur	4	4	5	4	0						
Macaque	8	8	7	8	5	0					
Marmoset	7	7	8	7	5	7	0				
Night monkey	7	7	8	7	3	8	4	0			
Spider monkey	6	6	7	6	4	9	6	4	0		
Squirrel monkey	9	9	10	9	7	11	6	6	6	0	
Slow loris	11	11	12	10	10	12	11	11	12	12	0

TABLE 1-17

Amino acid differences between the myoglobins within primates (Romero-Herrera *et al*. 1973, 1974).

	Man	Chimp	Gib	Bab	Mac	Woolly	Squ	Mar	Gal	Lem	Tree
Man	0										
Chimpanzee	1	0									
Gibbon	1	2	0								
Baboon	6	7	5	0							
Macaque	7	8	6	1	0						
Woolly Monkey	16	17	15	13	12	0					
Squirrel Monkey	17	18	16	12	12	4	0				
Marmoset	14	15	13	11	10	4	4	0			
Galago	23	24	24	22	21	21	23	23	0		
Sportive lemur	22	21	23	21	21	19	17	17	21	0	
Tree shrew	13	14	14	12	12	17	17	17	16	14	0

C. Discussion

1. PRIMATE EVOLUTION

The accumulation of evidence from macromolecules on the extent of differences among primates at the genetic level now permits a comparison of results from various methods. In the main, the macromolecular data are in agreement as to the cladistic or branching relationships of the various primates. This should not be surprising if what is being assayed by these techniques is some approxiamtion of a "true" or "real" genetic distance. Below will be presented the various phylogenics constructed from the data presented in the previous section. Certain problems in interpretation of the data will also be duscussed. The discussion will center on 1) the overall perspective - the major lineages, 2) the anthropoidea, and 3) the Hominoidea. The major point of this section is to emphasize the fact that when taken as a whole, the molecular data provide a fairly clear and consistent picture of the evolutionary relationships of the modern primates.

The Major Lineages

The ability to resolve lineages with great accuracy rests on two factors. First, and this is not always possible, there should be many separate lineages or clusters of separate lineages along a major phyletic branch. The separation provides the opportunity to either purify antigens and produce antisera directed to these antigens from an array of forms within the groups along the major lineage, or to sequence protein from many different forms within the group. The first step in an immunological study would then be to clarify the within-group analysis using the antisera prepared to both the antigens of species within the group and to antigens of species outside the group. Reciprocal measurements yield a more precise estimate of the antigenic differece between groups. These outside measurements provide different perspectives of the major lineage. Monotypic taxa with a long independent lineage along which have occurred large amounts of change and where antisera are not available, are among the most difficult lineages to resolve. The same problem exists in protein sequence studies as it is sometiemes difficult to assay all of the substitutions that have occurred in a particular protein because of back mutations or because multiple hits at a specific codon remain unseen. Without other closely related sequences to compare, it is hard to know with great exactitude the "true" sequence of events that occurred along the major lineage. The more sequences available, the greater the chance of detecting back mutations and parallel mutations and multiple hits at a codon. *Tarsius*, a monotypic lineage, is an example of a form whose placement has proven difficult.

The macromolecular data in general suggests that the primates, including the Anthropoidea, Lemuriformes and Lorisiformes, are a group relative to any other mammalian group. Protein sequence studies including fibrinopeptide (Wooding and Doolittle 1972), myoglobin (Romero-Herrera 1973) and alpha and beta haemoglobin (Goodman *et al*. 1974) seem to indicate that the primates share a monophyletic lineage along which occurred a number of substitutions. Although in some cases involving the haemoglobins, the evidence is not as clear as with the former two molecules.

The micro-complement fixation data suggest that these primates named above share a fairly long common lineage along which accumulated a large number of substitution in both albumin and transferrin. There are five major lineages that can be resolved given the present immunological data. The five lineages appear to radiate from a common node and include the Anthropoidea, the common Lorisiformes-Lemuriformes lineage, and the independent branches leading to *Tarsius*, *Tupaia* and *Cynocephalus* (Figure 1-4). *Tupaia* may be of a somewhat earlier radiation and the latter two are not usually considered primates, at least not taxonomically. The relevant immunological data are presented in Table 1-9.

The transferrin data indicate that the Lemuriformes and Lorisiformes share a short common lineage after the divergence of the lineages leading to other primate forms. The albumin data only weakly associate the two groups with the exclusion of the other lineages. Romero-Herrera (Romero-Herrera *et al.* 1973) based on data from myoglobin sequences, associates the two with a few substitutions occurring along a common lineage. Dene (Dene et al. 1976) using immunodiffusion also detects this common lineage.

The case for inclusion of *Tupaia*, *Tarsius*, and *Cynocephalus* in the clade primates, not necessarily taxonomically, is strengthened by the fact that the transferrins of these forms cross react strongly with antisera directed against the transferrins from species which are normally classified as primates. From a primate anti-transferrin perspective, only certain rodents and carnivore transferrins cross react. The latter cross reactions are extremely weak. The transferrins of no other order of mammals cross react with primate anti-transferrins.

Goodman (Goodman 1973; Goodman *et al*. 1974) , on the basis of immunological data, places *Tupaia* outside the primates. It is, however, the closest nonprimate lineage. On the basis of its myoglobin sequence *Tupaia* cannont be placed either inside or outside the clade primates. (Romero-Herrera *et al*. 1974) Dene *et al*. (1975) place *Cynocephalus* as a lineage that is outside the primates in a similar position as *Tupaia*. *Tarsius* is associated with the Anthropoidea in a taxon (semiorder) Haplorhini (Goodman 1973; Goodman *et al*. 1974). At the present moment, the existence of a common *Tarsius* and anthropoid lineage can not be documented with the albumin and transferrin immunological data. Recent preliminary evidence on the alpha and beta haemoglobin sequences from Tarsius suggest that it is not cladistically closer to either the Anthropoidea or to the remaining prosimians; it is however a primate.

The molecular data indicates that if *Cynocephalus* and *Tupaia* are not strictly cladistic primates, then they would be the closest outside species to the group normally considered primate, usually the Anthropoidea, *Tarsius* and the Lemuriformes - Lorisiformes. It is unclear as yet, if any of these lineages seems slightly more closely related to any of the other lineages (except for the Lemuriformes - Lorisiformes group). There does not appear to be a strong association of any pair of these major lineages. Yet, we cannot conclude with certainty that this association does not exist. Only more molecular data will clarify the problem of resolving whether these necessarily short lineages existed. From morphological consideration, McKenna (1974) has recently proposed that the orders Dermoptera (*Cynocephalus*), Tupaioidea and Primates be grouped together in the superorder Archonta Simpson 1945.

Anthropoid Evolution

Given the data, it is readily apparent that the Anthropoidea is composed of three clusters of species, including the Hominoidea, the Cercopithecoidea and the Ceboidea. The former two are closer to each other by almost every molecular measure, except for the primate lysozyme data, than they are to the latter group the Ceboidea. Reciprocity problems are inherent in the lysozyme / anti-lysozyme system as has been pointed out (Prager et al. 1974). The overwhelming evidence is that the Catarrhini are a unit relative to the Platyrrhini.

All the molecular data support the conclusion that the Anthropoidea share a common lineage subsequent to the divergence of any prosimian stock. Along this lineage accumulated some 70 units of combined albumin and transferrin units of change, three myoglobin sequence changes, seven fibrinopeptide changes, five beta haemoglobin changes and two units of antigenic distance; all before the divergence of the New World monkeys.

The Ceboidea form a fairly tight unit evolutionary radiation with a division into units the Callithricidae plus Callimico and a number of other fairly independent ceboid lineages (Cronin and Sarich 1975; Baba et al. 1975; Boyer et al. 1971).

The Catarrhini form a group relative to the Platyrihini, with respect to serum proteins, albumin and transferrin (Sarich 1970; Sarich and Cronin 1975), prealbumin, albumin alpha 2 macroglobulin, thryglobulin, transferrin, ceruloplasmin and gamma globulin (Goodman et al. 1979), DNA (Kohne 1972), myoglobin (Romero-Herrera 1973), haemoglobin (Goodman et al. 1973, 1974), fibrinopeptides (Wooding et al. 1972) and carbonic anhydrase (Nonno et al. 1969).

The Catarrhini are traditionally broken into two taxonomic units, the Hominoidea and the Cercopithecoidea on morphological grounds. This is also true with respect to the molecular division. The Cercopithecoidea have had little detailed genetic work, yet it is apparent that the basic division into leaf eaters (Colobinae) and non-leaf-eaters (Cercopithicine) is recoginzed at the molecular level (Sarich 1970; Banicot and Wade 1970, Goodman and Moore 1971). A detailed presentation of the evolution of the Cercopithecoidea as determined by the micro-complement fixation technique is in preparation (Cronin and Sarich 1976) and a brief preliminary version is in press (Sarich and Cronin 1975).

Hominoid Evolution

The Hominoidea are similar to each other in amino acid sequences of haemoglobins, myoglobin, fibrinopeptides, carbonic anhydrases, and in DNA. The immunological data also make it apparent that the Hominoidea is a tight knit group. Traditional taxonomy has divided the Hominoidea into three groups separated from each other, usually at the family level, the Pongidae (sometimes including the subfamily Hylobatinae) the Hominidae, and the Hylobatidae (if not included in Pongidae.)

The immunological and sequence data, as well as the DNA data, clearly support an early divergence of the gibbon lineage. However, a major question in hominoid cladistics evolution is the position of Pongo, the orang, vis a vis the other lineages. MC'F studies seem to indicate that the orang diverges approximately at the same time the gibbon lineage diverges from the lineage leading to man, chimpanzee and gorilla.

The DNA data of Hoyer (Hoyer et al. 1972) also supports this evolutionary position of the orang. On the other hand, the immunodiffusion data and the fact that the orang seems to share along with man, chimpanzee and gorilla, a change at position 4 in fibrinopeptide A, suggests that the orang may be somewhat cladistically closer to man, chimpanzee and gorilla. Recent sequence data with respect to orang myoglobin is ambiguous.

It appears that there is a common lineage leading to a three way divergence of man, chimpanzee and gorilla subsequent to the divergence of the Hylobates and Pongo lineages. Along this lineage acculULates some 4 albumin units, 8 transferrin units, some 2% DNA sequence change, two fibrinopeptide substitutions, two carbonic anhydrase substitutions, two beta globin changes, one myoglobin change, and about one unit of antigenic distance.

There appears to be no association of chimpanzee and gorilla after the divergence of the lineage leading to man. Since the three lineages have separated, they have accumulated about 4 transferrin units, 3 albumin units, 2 haemoglobin substitutions along the gorilla lineage; one myoglobin change along the chimpanzee lineage; and one haemoglobin substitution on the human lineage. No fibrinopeptide substitutions have occurred on any of the three lineages.

The DNA data is of little use here, as the studies of Kohne et al. (1972) failed to include Gorilla. In the study of Hoyer et al. (1972), Pan and Homo appear to be somewhat closer. Yet from the perspective of Pongo, the Gorilla DNA seems to have evolved more; so that Homo and Pan may not be actually cladistically closer but may only appear so because

Gorilla has diverged more than Homo or Pan. An electrophoretic survey of Gorilla proteins would prove useful as would a cladistic analysis of chromosomal evolution (i.e. translocations, inversions, deletions, etc.) in Pan, Homo and Gorilla. In summary, all molecular evidence suggests that man, chimpanzee and gorilla are a monophyletic lineage, and that all are extremely similar at the genetic level. In fact, because of their close genetic similarity and the cladistic relationship among the African apes and man, Goodman (1962, 1963a, 1963b) has suggested that the African apes be removed from the Pongidae and placed within the Hominidae in the subfamily Homininae (Goodman and Moore 1971).

FIGURE 1-4

A phylogenetic analysis of the major primate lineages based on the albumin and transferrin immunological distances of Table 1-9. The numbers above the lines indicate the number of albumin plus transferrin units of change allocated to that lineage. The bats are included as probably one of the closest groups to the primates. The time scale is drawn using the relationship of 125 units of albumin plus transferrin change per 60 million years along an average mammalian lineage.

FIGURE 1-5

A transferrin cladogram of the Anthropoidea constructed according to the method described in the text and in Figure 1-3. The immunological distances on which this phylogeny is based are those of Table 1-10. The percent standard deviation is 8.9%. The number in parenthesis following the species names represents the amount of transferrin immunological distance accumulated on the species' lineage from the node separating the catarrhines and platyrrhines.

FIGURE 1-6

A DNA cladogram of the primates constructed according to the method detailed in the text. The DNA differences on which this is based are taken from Table 1-2. The numbers above the lineage represent percent nucleotide substitution occurring along that lineage.

FIGURE 1-7

A cladogram of the primates based on the immunodiffusion data. Differences are expressed as antigenic distance units. (Adapted after Goodman and Moore 1971).

FIGURE 1-8

A fibrinopeptide cladogram of 12 primates. The numbers above the lineages represent numbers of amino acid substitutions occurring in fibrinopeptide A and B along that lineage. (Adapted after Wooding and Doolittle 1972).

FIGURE 1-9

An alpha haemoglobin cladogram of 10 primates. The numbers above the lineages represent numbers of amino acid substitutions occurring along that lineage. The cladogram was constructed by the maximum parsimony method. (Adapted after Goodman _et al_. 1972).

FIGURE 1-10

A beta haemoglobin cladogram of 12 primates. The numbers above the lineages represent numbers of amino acid substitutions occurring along that lineage. The cladogram was constructed by the maximum parsimony method (Adapted after Goodman *et al*. 1972).

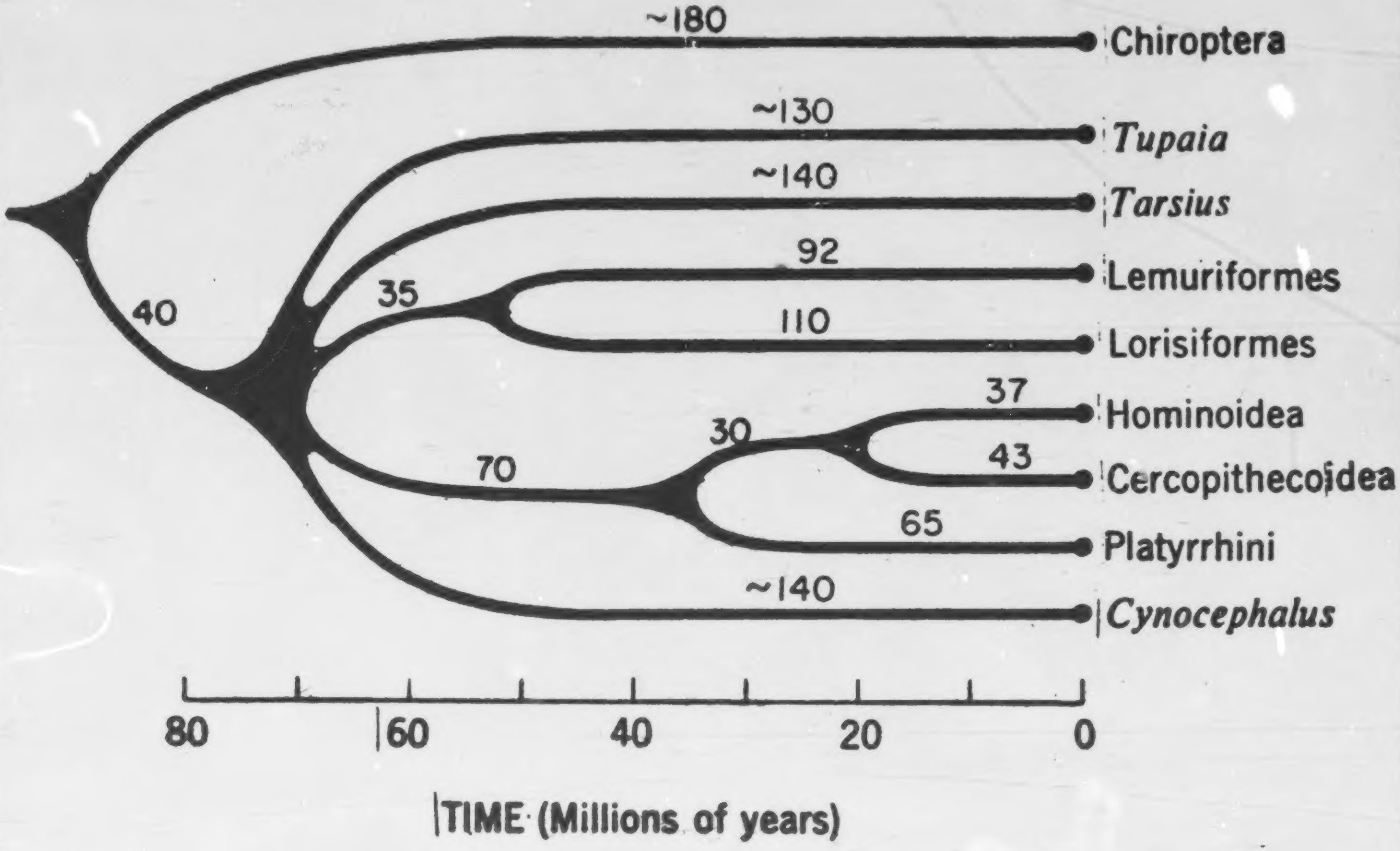
FIGURE 1-11

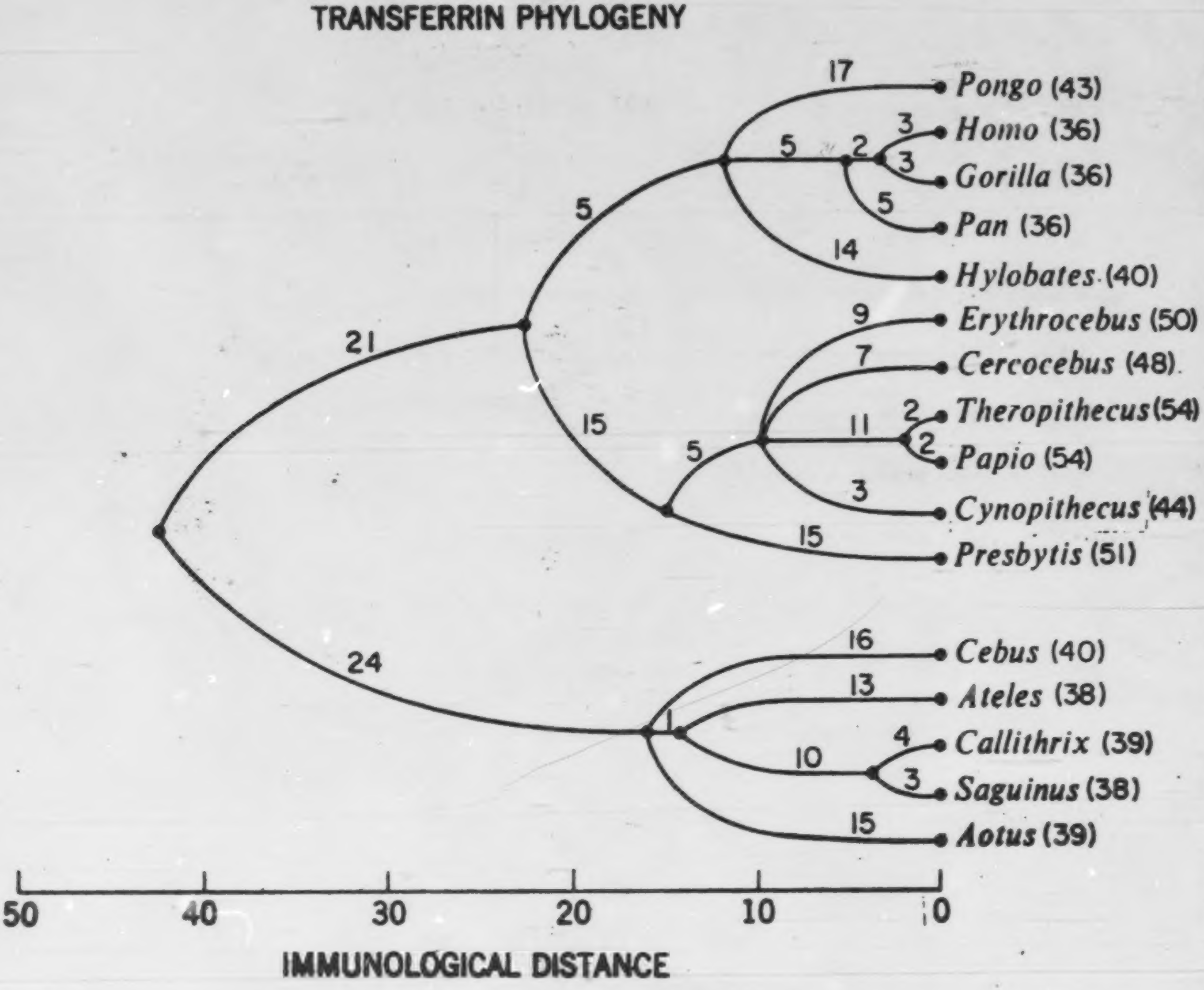
A myoglobin cladogram of 10 primates. The numbers above the lineages represent number of amino acid substitutions occurring along that lineage. (Adapted after Romero-Herrera *et al*. 1973).

FIGURE 1-12

The combined albumin, transferrin and DNA phylogeny of the Hominoidea. The numbers on the lineages are, in order, the number of albumin and transferrin units of change, and the Δ Tree times 10 for that lineage. Data is drawn from Tables 1-2, 1-3. 1-10- 1-11

ALBUMIN PLUS TRANSFERRIN PHYLOGENY OF PRIMATES AND RELATED MAMMALS


~180
Chiroptera
~130
Tupaia
~140
Tarsius
92
Lemuriformes
35
40
110
Lorisiformes
37
Hominoidea
30
43
Cercopithecoidea
70
65
Platyrrhini
~140
Cynocephalus
80
60
40
20
0
TIME (Millions of years)


TRANSFERRIN PHYLOGENY
Pongo (43)
Homo (36)
Gorilla (36)
Pan (36)
Hylobates (40)
Erythrocebus (50)
Cercocebus (48)
Theropithecus (54)
Papio (54)
Cynopithecus (44)
Presbytis (51)
Cebus (40)
Ateles (38)
Callithrix (39)
Saguinus (38)
Aotus (39)
IMMUNOLOGICAL DISTANCE

DNA PRIMATE PHYLOGENY

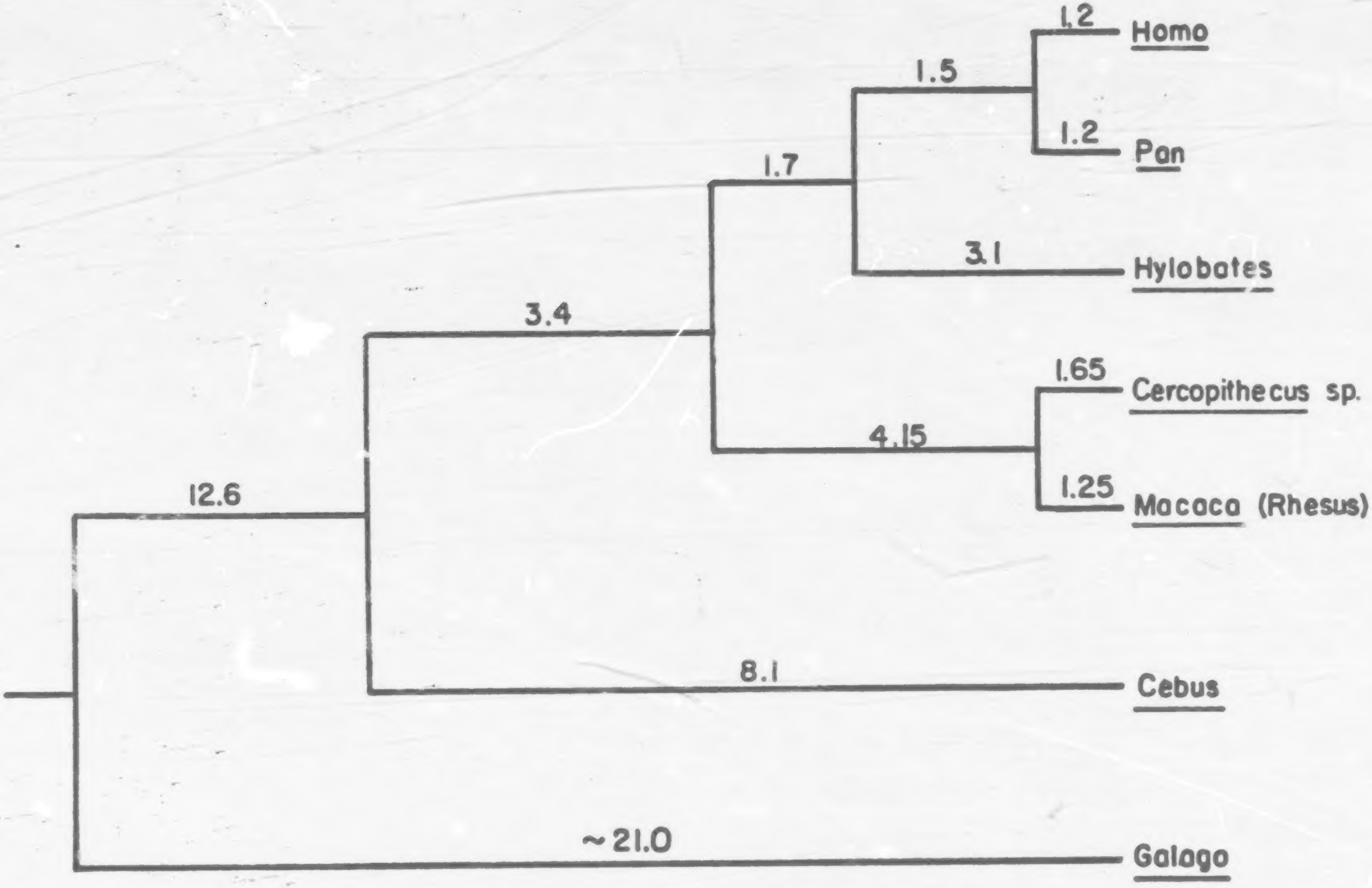

1.2
Homo
1.5
1.2
Pan
1.7
3.1
Hylobates
3.4
1.65
Cercopithecus sp.
4.15
1.25
Macaca (Rhesus)
12.6
8.1
Cebus
~21.0
Galago

FIGURE 1-6

PRIMATE IMMUNODIFFUSION PHYLOGENY

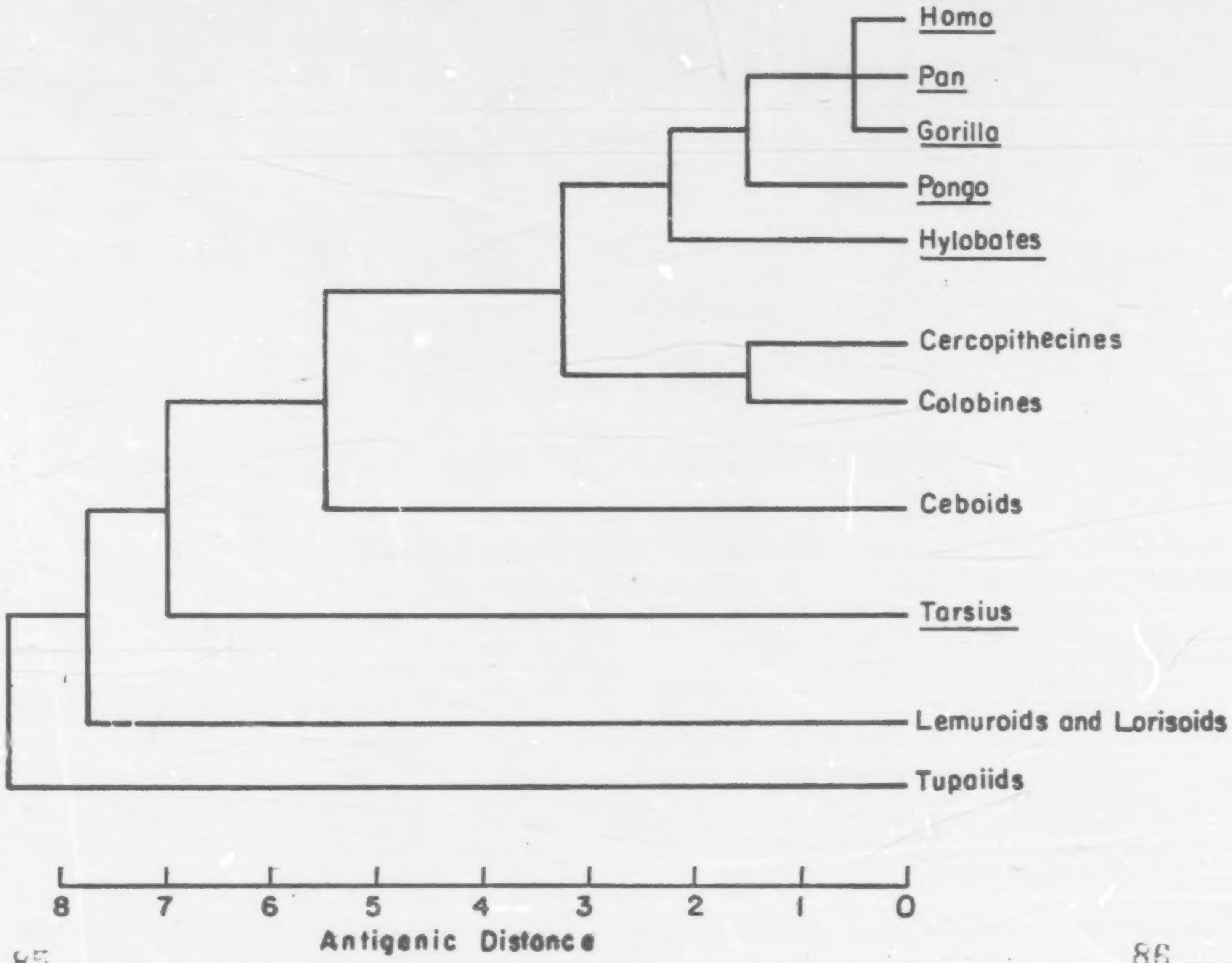
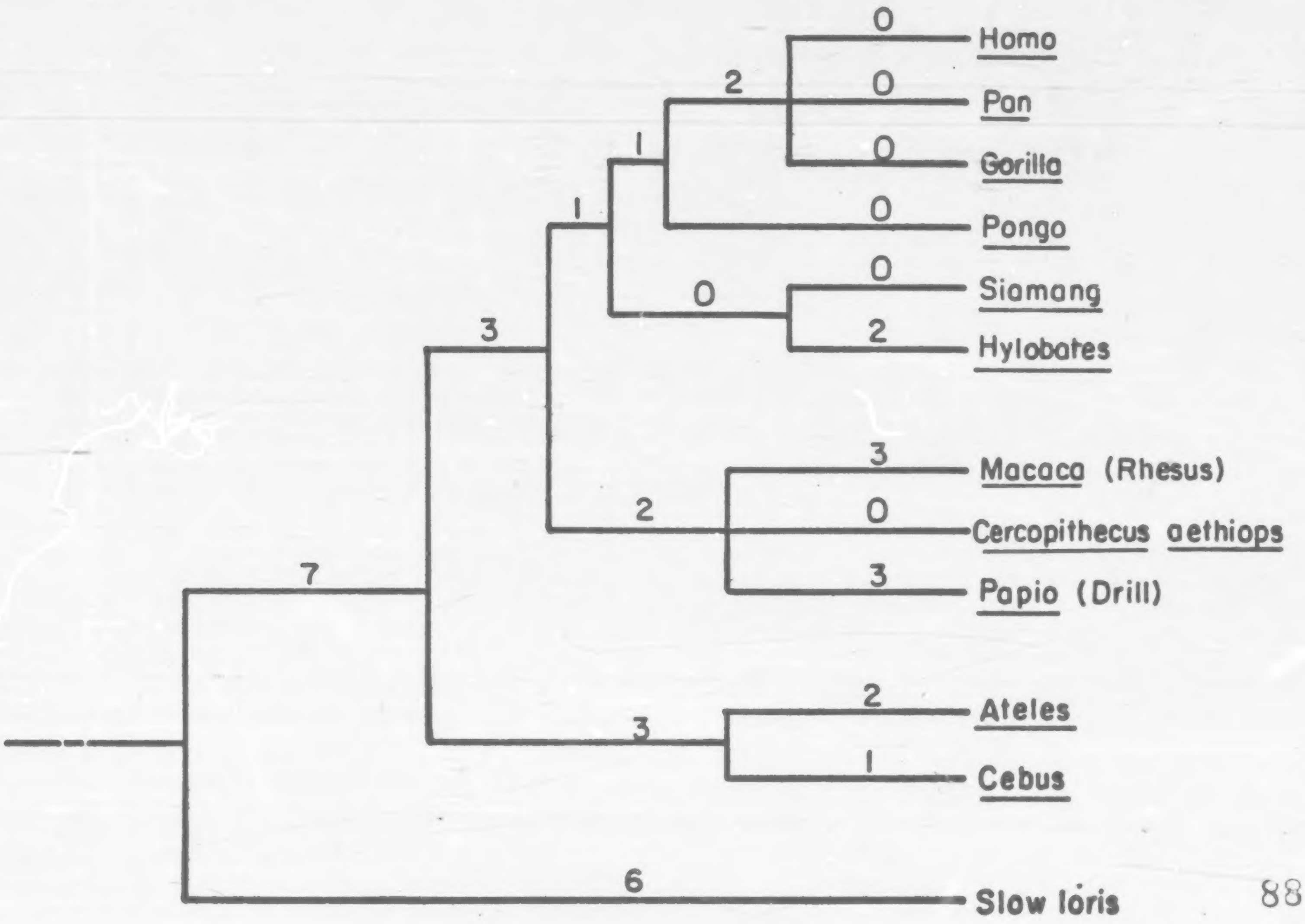

Homo
Pan
Gorilla
Pongo
Hylobates
Cercopithecines
Colobines
Ceboids
Tarsius
Lemuroids and Lorisoids
Tupaiids
8
7
6
5
4
3
2
1
0
Antigenic Distance

FIGURE 1-7


PRIMATE FIBRINOPEPTIDE (A+B) PHYLOGENY

0
Homo
2
0
Pan
1
0
Gorilla
1
0
Pongo
0
0
Siamang
3
2
Hylobates
3
Macaca (Rhesus)
2
0
Cercopithecus aethiops
7
3
Papio (Drill)
2
Ateles
3
1
Cebus
6
Slow loris

FIGURE 1-8

PRIMATE ALPHA HAEMOGLOBIN PHYLOGENY

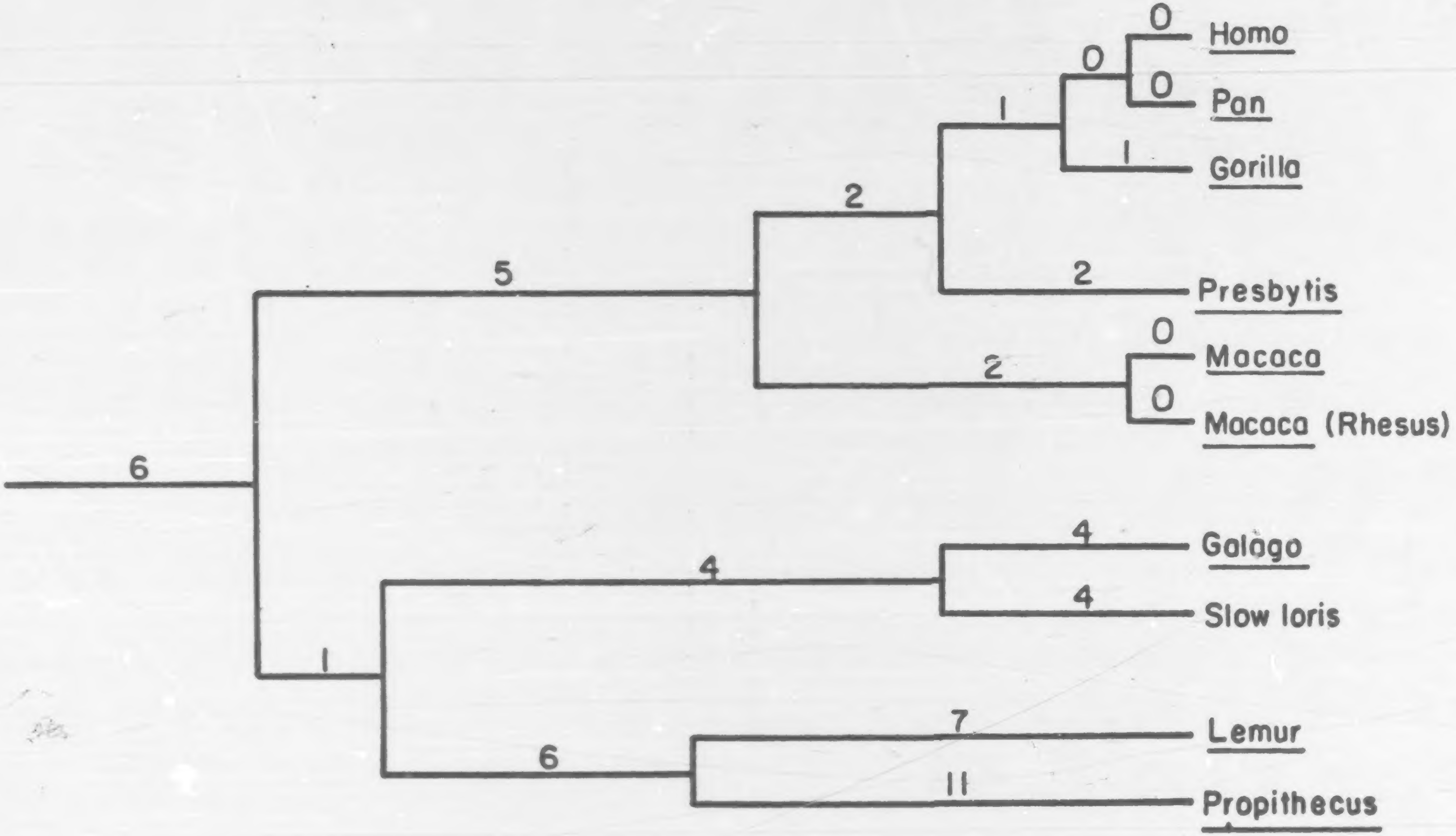
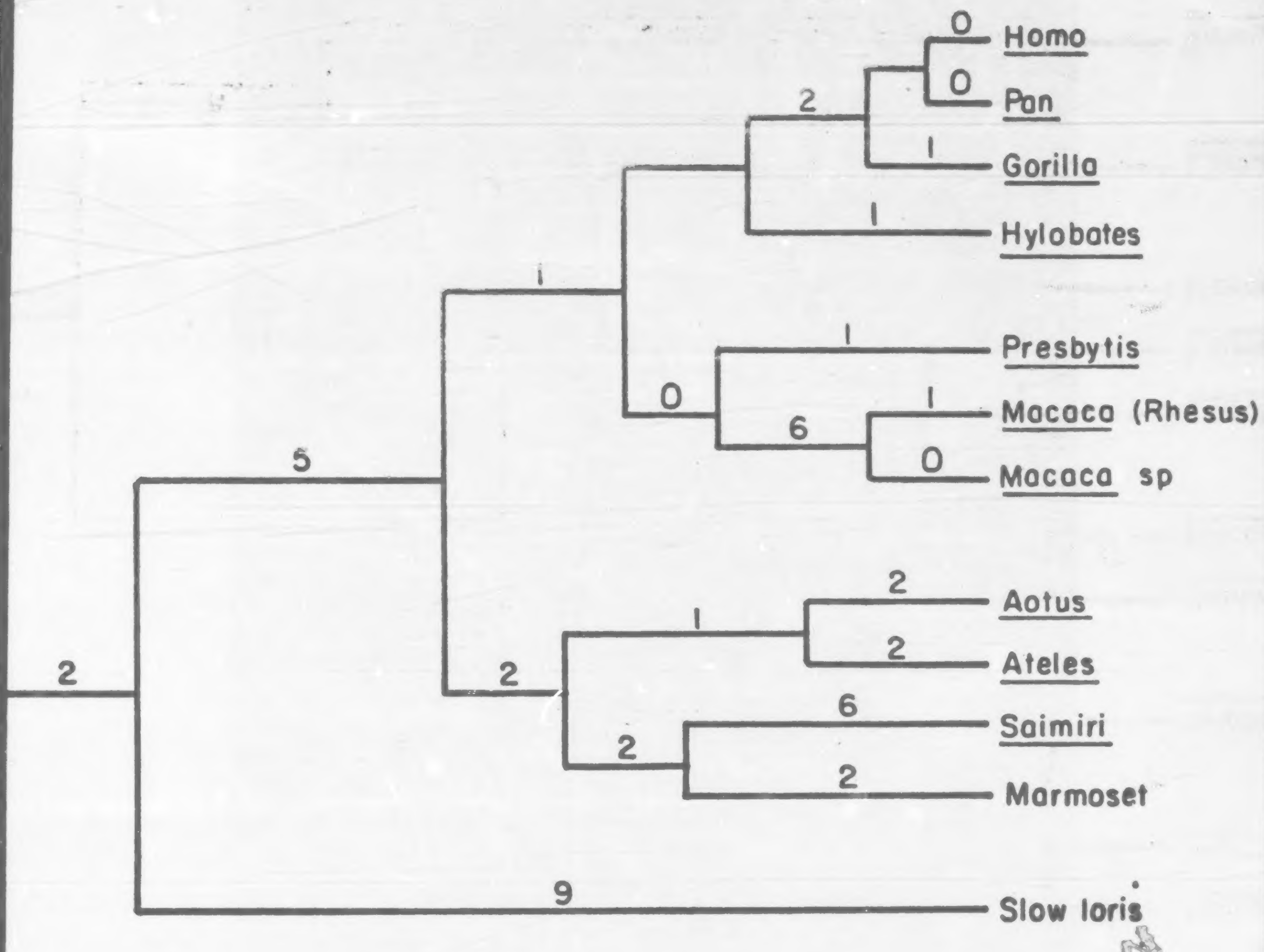

0
Homo
0
0
Pan
1
1
Gorilla
2
5
2
Presbytis
0
Macaca
2
0
Macaca (Rhesus)
6
4
Galago
4
4
Slow loris
1
7
Lemur
6
11
Propithecus

FIGURE 1-9

PRIMATE BETA HAEMOGLOBIN PHYLOGENY


0
Homo
0
Pan
2
1
Gorilla
1
Hylobates
1
1
Presbytis
0
1
Macaca (Rhesus)
6
0
Macaca sp
5
2
Aotus
1
2
Ateles
2
2
6
Saimiri
2
2
Marmoset
9
Slow loris

MYOGLOBIN PRIMATE PHYLOGENY

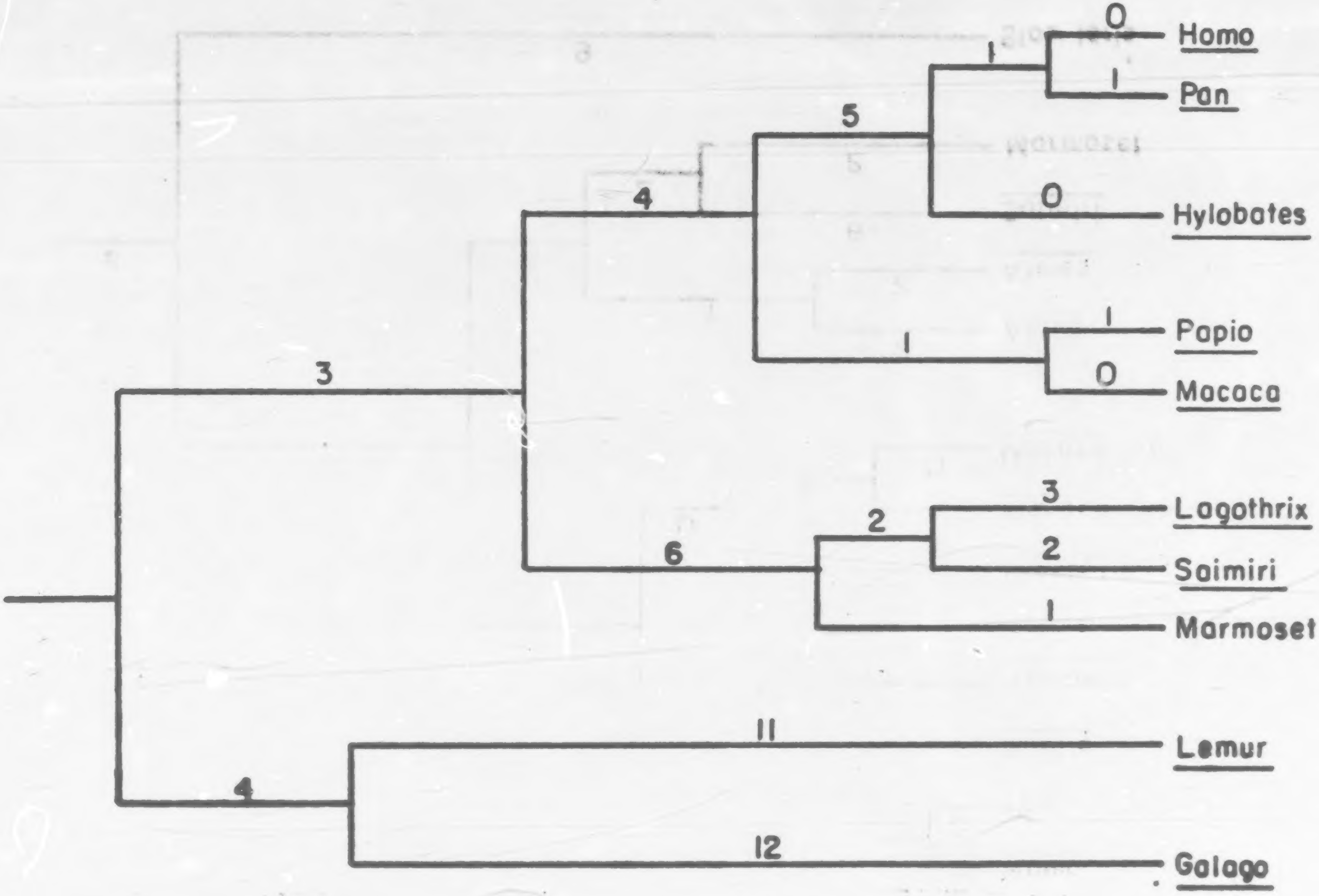
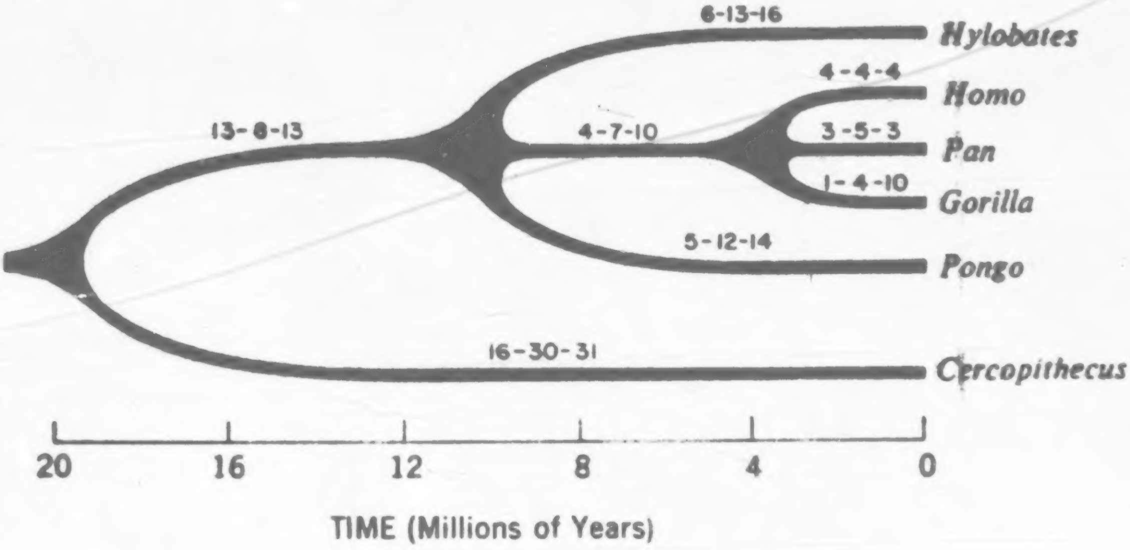

0
Homo
1
Pan
1
5
0
Hylobates
4
1
Papio
1
0
Macaca
3
3
Lagothrix
2
2
Saimiri
6
1
Marmoset
11
Lemur
4
12
Galago

FIGURE 1-11

FIGURE 1-12

ALBUMIN, TRANSFERRIN, AND DNA PHYLOGENY OF THE HOMINOIDEA


6-13-16
Hylobates
4-4-4
Homo
13-8-13
4-7-10
3-5-3
Pan
1-4-10
Gorilla
5-12-14
Pongo
16-30-31
Cercopithecus
20
16
12
8
4
0
TIME (Millions of Years)

2. TIME SCALE FOR PRIMATE EVOLUTION

Calibration of an Immunological Clock

It appears that albumin accumulates approxiamtely 50 units of change per sixty million years per lineage or 100 units per sixty million years of separation. Similar results have been found for a large variety of vertebrates, carnivores (Sarich 1969), ranid frogs (Wallace et al. 1973), hylid frogs (Maxson 1973; Maxson and Wilson 1975), and iguanid lizards (Gorman et al. 1971).

Transferrin accumulates about 150 units per sixty million years of separation in mammalian and snake lineages (Mao et al. 1971; Cronin and Sarich 1972, 1975 in press; Sarich 1974). In birds the rate of transferrin evolution is one quarter to one half that found in mammals and snakes. Similiar results are observed in serum albumin with a rate of evolution equal to one third that found in mammals (Prager et al., 1974). This phenomenon of an evolutionary deceleration in birds is not unique to these two molecules. Lysozyme and cytochrome C seem to evolve twice as slowly in birds as in mammals (Prager et al. 1974). This problem points to the fact that rates of evolution cannot be assumed; they must be calculated for every group under study.

In the equation Immunological Distance = K x Time (10^6 year), K approximates 1.67 for albumin and 2.5 for transferrin per million years for mammalian lineages. Thus, 250 units of combined albumin plus transferrin immunological distance calibrates to approximately sixty million years. Using this calibration point for albumin and transferrin, it can be seen in Table 1-17 what the times of separation of various taxa are for the two molecules both independently and averaged. There is a close agreement between what either molecule alone predicts

Table 1-18 lists the relative genetic distances between the same taxa when other molecules are compared. The molecular data when considered as a whole support the hypothesis that the immunological data is not unique or unrepresentative of such macromolecular evidence. Dates of divergence between the taxa listed are easily calculated given the date. The data in Table 1-18 correlated at the 0.96 level. A manuscript is in preparation to detail these genetic distances (Cronin, Sarich and Dempster in prep.).

The dates of divergence calculated from the immunological data presented in this study are in agreement with dates proposed by Sarich 1970; Sarich and Wilson, 1967a, 1967b; Wilson and Sarich, 1969. Certain differences are, however, apparent. It was postualted that prosimians and anthropoids differed by about 100 albumin units. This figure has had to be adjusted upwards given the addition of five new lemurid albumin antisera. A further point of difference is the date of 30 million years for the hominoid-cercopithecoid divergence used to calculate the man-chimpanzee divergence time of 5 million years (Sarich and Wilson 1967b).

In subsequent publications, a divergence time of approximately 22 million years has been estimated for the hominoid-cercopithecoid separation (Sarich 1970, 1971). The date estimated by transferrin of 18 million years is close in agreement with this latter figure.

TABLE 1-17

Times of Divergence Among Various Primate Taxa Predicted by Albumin and Transferrin Immunological Distances

Taxa	Time of Divergence (10^6 yrs.)[a]		
	Albumin	Transferrin	Average
Homo vs *Pan* vs *Gorilla*[b]	3.6	4	3.8
Homo vs *Pongo* vs *Hylobates*[b]	[illegible]	9.6	8.4
Colobinae vs Cercopithecinae	14.4	10.8	12.6
Hominoidea vs Cercopithecoidea	22.2	18	20.1
Platyrrhini vs Catarrhini	34.2	33.6	33.9
Anthropoidea vs Prosimii	70.2	64	67.1

[a] Times of divergence are calculated on the basis that approximately 100 albumin and 150 transferrin units accumulate between two taxa over sixty million years.

[b] The taxa listed are cladistically equally divergent from a common node so that it is a three way comparison. Since all three lineages separated cladistically from the same node, they have existed for equal evolutionary time.

TABLE 1-18

Relative Molecular Differences Among Various Primate Groups Referred to a Catarrhine-Platyrrhine Distance of 1.0

Groups Compared	Albumin[a]	Transferrin[b]	DNA[c]	Mixed Immunology[d]	Myoglobin[e]	Fibrinopeptides[f]	Beta Haemoglobin[i]	Carbonic Anhydrase[j]	Lysozyme[k]
Homo vs *Pan*	0.12	0.13	0.15	0.12	0.08	0	0	.05	0
Homo vs *Pongo* vs *Hylobates*[g]	0.25	0.30	0.33	0.29	NA[h]	0.3	.43	NA	NA
Hominoidea vs Cercopithecoidea	0.58	0.53	0.61	0.53	0.5	0.5	.85	.65	.90
Catarrhini vs Platyrrhini	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
Anthropoidea vs Prosimii	2.1	1.8	2.6	1.67	1.5	1.8	1.57	1.73	1.45

[a] From Sarich (1970) and subsequent work in this laboratory. The number is immunological distance between the groups divided by the catarrhine-platyrrhine albumin immunological distance.

[b] Data from this laboratory and expressed as in a.

[c] Calculated from the data in Hoyer *et al*. (1972) and Kohne, Chiscon, and Hoyer (1972) by dividing the ΔT_m for the groups by the corresponding catarrhine-platyrrhine value.

[d] From Goodman and Lasker (1973).

[e] From Romero Herrera and Lehmann (1973). The calculations are based on amino acid differences.

[f] From Wooding and Doolittle (1972; Tables 1 and 2). The calculations are based on amino acid differences

[g] The taxa listed are cladistically equally divergent from a common node so that it is a three-way comparison.

[h] The amino acid sequence of *Pongo* myoglobin is unknown.

[i] From Goodman and Lasker (1973). The data presented is based on amino acid differences found between the taxa.

[j] From Nonno *et al*. (1969).

[k] From Hanke *et al*. (1973; Table 11). Only the data gathered with the anti human lysozyme is included.

This earlier publication (Sarich and Wilson 1967b) assumed a hominoid-cercopithecoid divergence time of approximately 30 million years. From this date, given the ratio of the man-chimpanzee albumin distance of 6-7 units, versus the hominoid-cercopithecoid distance of 35 I.D. units, and given the hypothesis of the regularity of protein evolution a time of divergence of 5 million years was calculated for man and chimpanzee. Additional albumin data have now been gathered. Given the 10 x 10 albumin catarrhine matrix (Table 1-11) a mean hominoid-cercopithecoid distance of 37 immunological distance units is obtained. A cladistic analysis of the hominoids indicates that man, chimpanzee, and gorilla diverged from a common node into three spearate lineages. Each lineage is a sample of the amount of change given that time of divergence for those lineages. A mean distance using all descendent lineages from a node may give a better representation of the actual distance between species descending from that node than only one measurement. This consideration gives a mean man-chimpanzee albumin distance of 6 units. The same analysis on the transferrin data reveals a mean man-chimpanzee immunological distance of 8. The hominoid-cercopithecoid mean is 45 transferrin units. The ratio is 1:6.1 for albumin and 1:5.6 for transferrin. Given the small distances involved between the great apes and man, the two ratios are consistent and predict that the human-chimpanzee divergence is somewhat less than four million years.

Objections to the Immunological Clock

Objections to the immunological clock usually stem from two sources. The first are objections based on the fact that the time scale of divergence of certain taxa seem to be at variance with certain interpretations of the fossil record. The second class of objections stems from a belief that either there is no basis for a clock, i.e., evolutionary rates are not constant, or that molecular evolution in certain lineages has decelerated. This slowdown can either be caused by a correlation of molecular evolution with generation length (shorter generation - faster rate of evolution or, vice-versa), or by certain physiological selective constraints. The main objectives to an immunological clock will be dealt with briefly below. These objections have been answered in the literature (Sarich 1973; Sarich and Cronin 1976).

Table 1-19 and Figure 1-14 are an adaptation from various sources presented by Simons (1969, 1974). Similar objections have been expressed by others (Uzzell and Pilbeam 1971; Leakey 1970). Simons, as can be seen in Figure 1-14, objects both at the cladistic level and the temporal level to the phylogenies presented in Figures 1-14 and 1-15. Figure 1-15 is adapted from Sarich (1970) and is shown first for a historical perspective and, secondly to show how the addition of the transferrin data has clarified and resolved certain problem areas.

Some object to the molecular clock based purely on paleontological consideration. For example, Simons believes that certain fossil forms are ancestral to specific living hominoids, including the following associations, 1) Ramapithecus - Homo, 2) Dryopithecus africanus - Pan, 3) Dryopithecus major - Gorilla and 4) Pliopithecus and Limnopithecus - Hylobates. Ramapithecus dates to about 14 million years, from the Miocene of East Africa. If this form is ancestral to Homo, then the divergence of the Hominidae and Pongidae occurred much before the 4-5 million years predicted by the immunological clock. Similarly if D. africanus and D. major are ancestral to chimpanzee and gorilla and date to 15-20 million years ago then the Pan-Gorilla divergence is minimally early to middle Miocene; again much greater than the immunological clock would suggest. Similarly, the gibbon divergence is dated to perhaps 30-35 million years ago. The Hominoid-Cercopithecoid split would be about 45 million and the Catarrhini-Platyrrhini divergence around 55 million. Though a rebuttal to each specific interpretation is not in order here, others, from a morphological viewpoint, have objected to the assignments of these forms to the lineages Simons has proposed (Morbeck 1972; Walker and Andrews 1973, Delson and Andrews 1975).

Some authors believe that the cladistics are correct but the clock is not accurate for various reasons. They believe that the molecular picture can be brought into accord with certain interpretations of the fossil record by recognizing that rates of molecular evolution are dependent on either generation length or upon the complexity of placentation. For example, Kohne (Kohne et al. 1972) has suggested that the close genetic relationship of man and chimp has been due to a retardation in the rate of genomic evolution in higher primates, not due to recent divergence times. Kohne et al. (1972) and Lovejoy et al. (1973) have postulated that generation length affects the rate of evolution. If mutations are primarily limited to DNA replication, then the number of replications occurring from germ line to gamete decreases per unit time as generation length increases. By assuming specific divergence dates for various taxa, Kohne, Table 1-21, calculates that the rate of nucleotide substitution since divergence of two lineages has decreased in higher primates due to increasing generation length compared to lower primates and short generation form mammals. Lovejoy has suggested (Lovejoy et al. 1973) that if these genetic distances are corrected by a generation length factor then times of separation of various taxa can be brought into accord with estimates of divergence times based on the fossil record. Similarly, Bauer (1973), Table 1-20, sees in immunodiffusion data times of divergence of taxa more in accord with proposed paleontological derived dates. Goodman, again assuming specific divergence times for various taxa, has suggested a slowdown in higher primates' rate of evolution. The causative mechanism would be selection against transplacental immunization (Goodman 1962, 1963a, 1963b; Goodman et al. 1971, 1972). Table 1-22 presents the sequence data interpreted in this manner.

Sarich and Wilson (1973) and Sarich (1972, 1973) have specifically dealt with the question of a slowdown in higher primate evolution. They suggest that the hypothesis of a deceleration is directly testable. They report that the amount of albumin evolution in higher primates is the same as in lower primates when lineages are measured from reference points outside the primates, Table 1-23. Short generation forms do not seem to accumulate more changes in albumin than do longer generation forms which is what the generation time model would predict. The amount of evolution occurring in the mouse lineage compared to that occurring in the man or chimpanzee lineage is the same. Yet, the generation times differ and have differed since the divergence of the mouse and human lineage by a significant amount (Sarich 1974).

Furthermore, they suggest that the DNA data and the sequence data can be interpreted to suggest that the rate of evolution of these molecules are linearly related to time. For example, if you suggest that the human-chimpanzee DNA difference accumulated in 5 M.Y then ask how long it took for the DNA differences to accumulate between other taxa, then the dates calculated agree extremely well with the immunologically predicted times. This would be true for every molecule in Table 1-18. Since the ratios of the genetic differences agree, predicted divergence dates should also agree.

It may be noted that the time of divergence of the various taxa within the primates are assumed. If you initially assume a long temporal separation between man and chimpanzee, and the genetic distance is small, then it might be logical, if not inevitable, to conclude that there has been a slow rate of evolution along the two lineages. However, the assumption of divergence dates, especially when a few million years is a significant proportion of the total lineage length, in order to prove there has been a slowdown in molecular evolution in higher primates, may be a circular argument. Sarich (1964) suggests that the phenomenon of a slowdown has never been demonstrated to have any existence independent of certain interpretations of the primate fossil record. Sarich reports that the concept of using molecules as a molecular clock is confirmed by direct testing of the clock hypothesis itself.

Two further criticisms of the molecular clock method have been put forward. These have both been answered in depth by Sarich (1974). Read and Lestrel (1970) have suggested that a log log model of the index of the dissimilarity vs. time is a better fit to the paleontological data than the semi-log model. Sarich (1974) has countered this by noting the nonpredictive nature of the log-log model and the fact the log-log model contradicts known capabilities in terms of the power of discrimination at the amino acid level, of the micro-complement fixation technique. Furthermore, direct immunological tests of avian lysozymes of known sequence suggests that the semi-log model gives an excellent fit to the date, Prager and Wilson (1971a, 1971b).

Uzzell and Pilbeam (1971) have suggested that the rate test as employed in MC'F to measure rates of evolution is insensitive. They suggest that as two species are separated for longer and longer periods of time the actual difference, in terms of sequence differences grows faster than the measured difference due to back mutations, parallel substitutions, and multiple substitutions at the same codon. Since MC'F measures amino acid differences, the method underestimates genetic distances by ever increasing amounts. Therefore, if the clock were set on a genetic distance at one end of the scale that is an underestimation of the actual genetic distance, then on the recent end of the scale, the genetic distances measured actually took less time to accumulate than the calculations would suggest.

Sarich (1974) presents data to counter this argument. He states that the MC'F technique, even at the end of the range of distances measurable by the technique, can discriminate between the amount of evolution that occurred along the Aotus compared to the Cebus lineage.

Aotus is some 20 units more conservative, less evolved, than the Cebus lineages. If there is a significant phenetic underestimation of the time phyletic genetic distance, then the further removed you are in an evolutionary sense (i.e., antibodies made to albumin from species further and further away evolutionarily) then the more this 20 unit difference would disappear. Because as you move away the less discrimination you expect because of multiple hits, parallel substitutions, etc. However, this is not the case. Hominoid reference antisera detect this 20 units as do prosimian anti-albumin and anticarnivore albumin. The latter immunological distances approach the operational limit of the MC'F technique. Thus, it is probable that the degree of phenetic underestimation of phyletic distance is relatively unimportant over the range of immunological distance, from 0-40% sequence difference, where the MC'F technique is operational. This is also suggested by the work of Prager and Wilson (1971a, 1971b) where there is a linear relationship of amino acid differences vs. immunological distance, ranging from 0-40% sequence difference. Most objections have been answered in print, and for a more detailed account of these answers to specific objections raised to the molecular clock hypothesis, as applied to primates, see Sarich (1972b, 1974); Sarich and Wilson 1973: and Sarich and Cronin (1976).

TABLE 1-19

Divergence dates of various primate taxa based on an interpretation of the fossil record. (Adapted after Simons 1969, 1972).

TAXA	Time of divergence x 10^6 years
Homonid-Pongid	~ 20-25
Pan-*Gorilla*	18-20
Pongidae-Hylobatidae	> 30
Hominoid-Cercopithecoid	~ 45
Catarrhini-Platyrrhini	~ 55
Prosimii-Anthropoidea	60-70

TABLE I-20

Times of divergence of various primate taxa based on a linear model of immunological relevant accepted mutation between species vs. time. Based on 28 different plasma proteins using immunodiffusion experiments. (Bauer 1973).

	Relative time units	Absolute time[1] 10^6 years
Homo	100	0.0
Pan	86.2	9.7
Gorilla	82.6	12.1
Pongo	77.5	15.7
Cercocebus	62.1	26.5
Macaca	61.0	27.3
Cercopithecus	58.0	29.4
Erythrocebus	57.3	29.9
Cebus	22.9	54.9
Galago	9.5	63.3
Eutheria	0.0	70.0

Time of divergence based on an assumption of a Eutherian Primate divergence of 70 million years ago.

TABLE 1-21

Rate of nucleotide substitution calculated in terms of absolute time. (Kohne *et al*. 1972)

DNA's compared	Millions of years of divergence	Total divergence time	% nucleotide substitutions since divergence	% change per 10^6 years	Nucleotide pair changes pe year
Man-Man	0	0	0	0	0
Man-Chimpanzee	15	30	2.4	0.08	1.6
Man-gibbon	30	60	5.3	0.09	1.8
Man-green monkey (G.M.)	45	90	9.5	0.1	2
Man-capucin	65	130	15.8	0.12	2.4
Man-galago	80	160	42	0.26	5.2
G.M.-G.M.	0	0	0	0	0
G.M.-rhesus	15	30	3.5	0.12	2.4
G.M.-man	45	90	9.6	0.11	2.2
G.M.-chimpanzee	45	90	9.6	0.11	2.2
G.M.-gibbon	45	90	9.6	0.11	2.2
G.M.-capucin	65	130	16.5	0.12	2.4
G.M.-galago	80	160	42	0.25	5.0

TABLE 1-22

Rates of substitutions of nucleotides in alpha and beta haemoglobin and fibrinopeptides in the time period of the origin of the eutheriacs to gorilla, chimpanzee, and man (Goodman et al., 1972)

Time period in 10^6 years	alpha haemoglobin # of nucleotide replacements	Rate 10^6 yrs.	beta haemoglobin # of nucleotide replacements	Rate 10^6 yrs.	fibrinopetide A + # of nucleotide replacements	Rate 10^6 years
90-65'	12	1 per 2	11	1 per 2	9 or 6	1 per 3 or 4
65-40	7	1 per 3.5	6	1 per 4	4	1 per
40-15	1	1 per 25	4	1 per 6	3	1 per 8
15 - gorilla, chimp, man	1,0,0	1 per 45	1,0,0	1 per 45	0,0,0	1 per 45

'Estimates of divergence times based upon interpretations from the fossil record. [Eutherian radiation 90 M.Y.; Primate radiation 65 MYBP; Hominoid-Cercopithecoid 40 M.Y.B.P.; Man-chimp-gorilla divergence 15 M.Y.B.P. (M.Y.B.P. = millions of years before present)]

TABLE 1-23

Three tests for the occurrence of an evolutionary slowdown in the hominoid lineage. (Sarich and Wilson 1973)

A. MC'F test with antisera to the albumins of four carnivore species.

Species	Mean I.D.
Homo sapiens	162
Macaca mulatta	166
Ateles geoffroyi	149
Nycticebus coucang	125
Lemur fulvus	135
Tarsius spectrum	137
Tupaia glis	156

B. Precipitin test with antiserums to the albumins of seven nonprimate species.

Species	Mean I.D.
Homo sapiens	169
Hylobates lar	169
Macaca mulatta	169
Aotus trivirgatus	150
Cebus capucinus	169
Nycticebus coucang	143
Lemur fulvus	150
Tupaia glis	163

TABLE 1-23 (continued)

C. MC'F test with antiserums to the albumins of five New World monkey species.

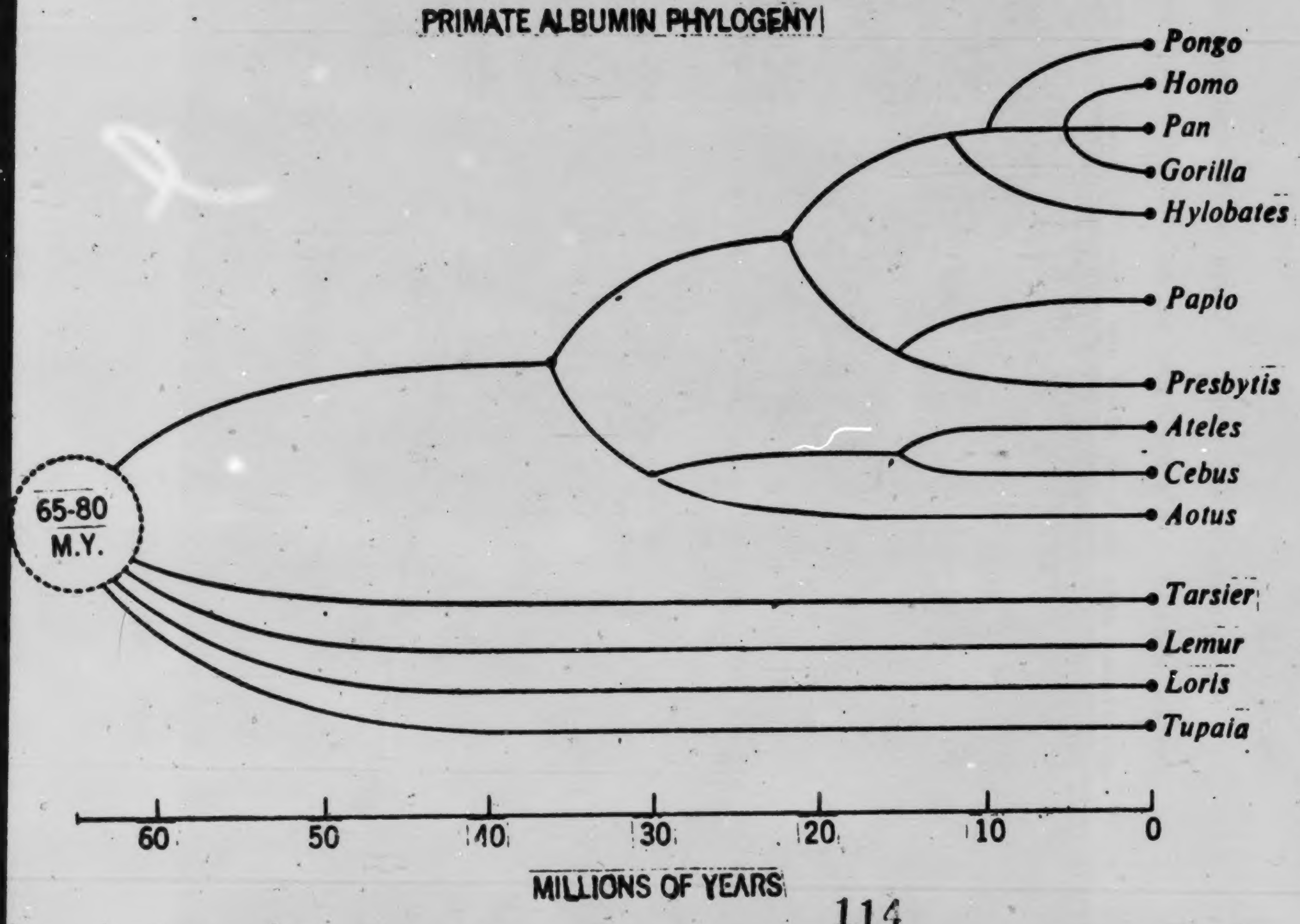
Species	Mean I.D.
Homo sapiens	55
Hylobates lar	53
Macaca mulatta	53
Presbytis entellus	52

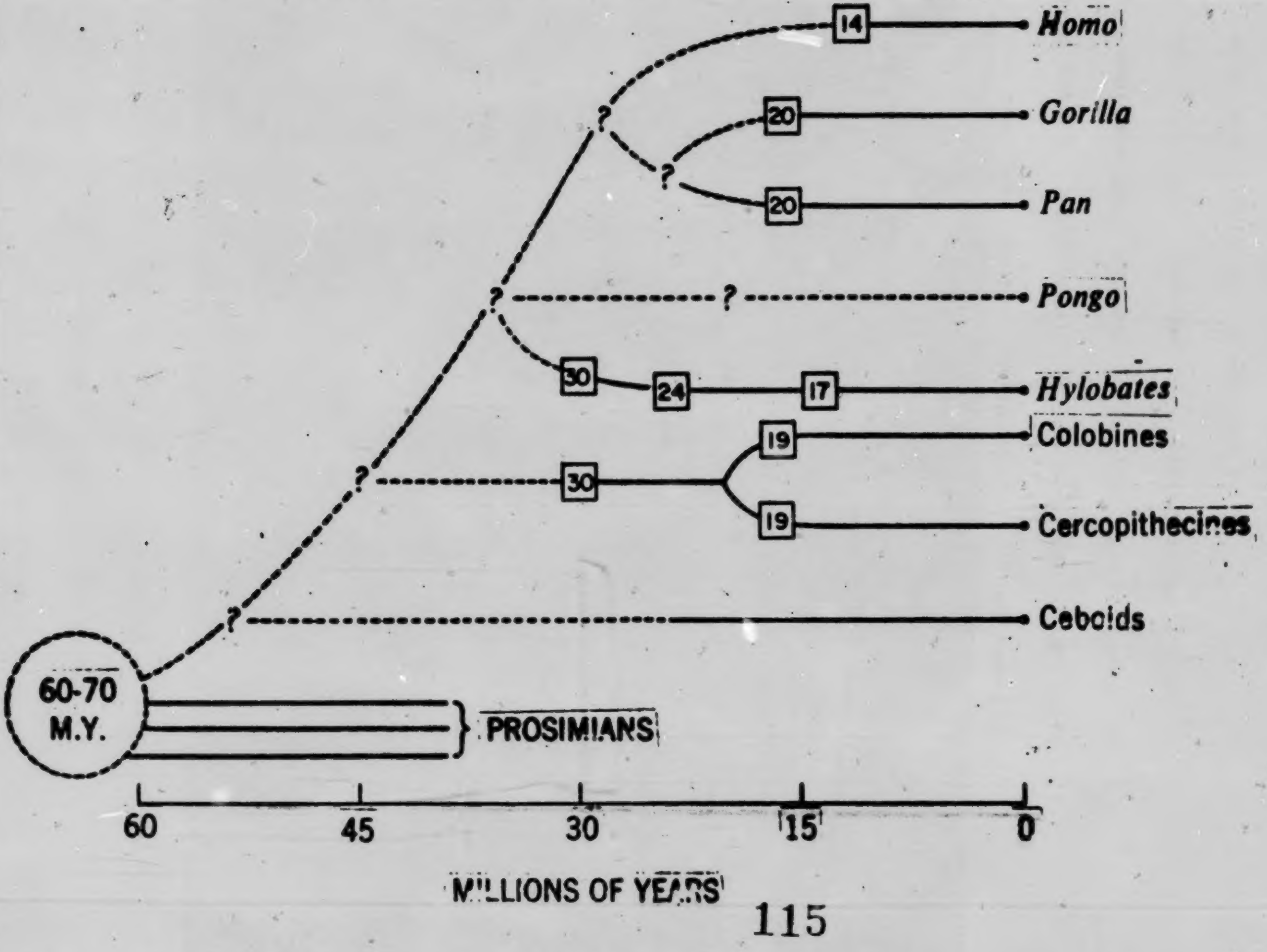
FIGURE 1-13

A phylogeny of the primates based on the evolution of the serum protein albumin. This phylogeny may be compared with Figure 1-4 where additional data has been added and resolving power increased. For example, a common Lemuriformes - Lorisiformes lineage is apparent with the addition of the transferrin data. Similarly, additional albumin and transferrin data suggest the orang (Pongo) lineage is part of a three way divergence, one lineage leading to Hylobates, and the second the common Pan, Gorilla, Homo lineage and the third the orang lineage. Thus, Pongo is not associated with the latter lineage subsequent to the gibbon's divergence as the earlier data suggested. (Adapted after Sarich 1970).

FIGURE 1-14

A phylogeny of the primates based on an analysis of the fossil record. Boxes with enclosed numerals along lineages indicate that a specific form is associated with that lineage at the approximate time so indicated by the numerals within the box. For example, on the lineage leading to Homo the boxed number 14 represents the form Ramapithecus dated to 14 million years ago, from East Africa. This form has been considered by some to be ancestral to Homo. (Adapted after Simons 1969, 1972).


PRIMATE ALBUMIN PHYLOGENY
Pongo
Homo
Pan
Gorilla
Hylobates
Papio
Presbytis
Ateles
Cebus
Aotus
65-80
M.Y.
Tarsier
Lemur
Loris
Tupaia
60
50
40
30
20
10
0
MILLIONS OF YEARS



Homo
Gorilla
Pan
Pongo
Hylobates
Colobines
Cercopithecines
Ceboids
PROSIMIANS
60-70 M.Y.
14
20
20
30
24
17
30
19
19
?
60
45
30
15
0
MILLIONS OF YEARS

3. Macromolecular Evidence Bearing on the Question of the Man-African Ape Divergence Time

The question of the ape-human divergence time is one of the most controversial of points. It has been known for some years how close the genetic relationships is between apes and humans (Goodman 1961,1962 1969a 1969b; Hafleigh and Williams 1966). Recent molecular work has confirmed earlier observation that man and apes are extremely closely related at the genetic level. These data include information from DNA studies, globin sequences, fibrinopeptide sequences, mixed immunology, and electrophoretic studies. Besides cladistic information, these data can yield estimates of the time of divergence of humans and apes.

King and Wilson (1975) as previously pointed out have surveyed proteins encoded by 44 loci using electrophoretic comparisons. The genetic distance between humans and chimpanzees is a very small one and on the order of the genetic distance found between sibling species of Drosophila or mammals. They further estimate that the average human polypeptide is more than 99% identical to its chimpanzee homologue. In fact, the probability that human and chimpanzee alleles are electrophoretically identical is 0.52%. This genetic distance yields an estimate of a time of divergence of humans and chimpanzees on the order of 4-8 million years (King 1973), Table 1-24.

Sequences of fibrinopeptides are available now for twelve primates including the five hominoid genera (Wooding et al. 1972). The sequences of fibrinopeptides A and B, a total of thirty resides, are identical for human, chimpanzee and gorilla. [illegible] possible to calculate an average

TABLE 1-24

Differences in amino acid sequences of human and chimpanzee polypeptides. The proteins with the postcript (1) have been compared immunologically; the remainder, by direct amino acid sequencing.

Protein	Amino acid differences	Amino acid sites
Fibrinopeptides A and B	0	30
Cytochrome C	0	104
Lysozyme[1]	~0	130
Haemoglobin (alpha)	0	141
Haemoglobin (beta)	0	146
Haemoglobin (A gamma)	0	146
Haemoglobin (G gamma)	0	146
Haemoglobin (delta)	1	146
Myoglobin	1	153
Carbonic anhydrase[1]	~3	264
Serum albumin[1]	~6	580
Transferrin[1]	~8	647
TOTAL	~19	2633

(Adapted after King and Wilson 1975.)

rate of substitutions found within the primates for the fibrinopeptides. All anthropoids must be equally separated in time from *Nycticebus*. Since these two taxa separated, there has been an average of 17 substitutions separating any anthropoid and *Nycticebus*. If it is assumed that prosimians and anthropoids separated approximately 70 million years ago then this works out to approximately one substitution per 4 million years. A separation time between human and chimpanzee of 15 million years or 30 million years total between the two forms would predict that the two forms would differ by some 7 substitutions. A direct ratio comparison of the genetic distance between *Homo* and *Hylobates* using the catarrhine-platyrrhine separation as a reference point indicates that *Homo* and *Hylobates* are .3 or 30% of the catarrhine-platyrrhine distance (Table 1-18). If we use a calibration point of 35 million years for the reference point, then *Homo* and *Hylobates* separated about 10.5 million years ago. (This is in agreement with the immunologically predicted date.) Since two mutations have occurred along the common *Homo*, *Pan*, *Gorilla* lineage this lineage must represent some time depth. Given the fact that the great apes and man do not differ in these sequences a range of 0 to 10.5 million years is indicated for the best estimate of the times of divergence.

The analysis of information from haemoglobin sequences may proceed in a similar fashion. An extensive number of alpha, beta, gamma and delta chain haemoglobin sequences are available from various species of primates (Goodman *et al*. 1971; Boyer *et al*. 1971). Man differs from chimpanzee in only one amino acid substutution in the delta chain (De Jong 1971a, 1971b). Man and chimpanzee both differ from *Gorilla* by one alpha and beta chain substitution. Averaging the distance between the three available prosimians (sifaka, Lemur and bush baby) and five anthropoid alpha sequences, 19 differences or substitutions are observed (Goodman *et al*. 1971). Assuming a prosimian-anthropoid divergence time of 70 million years, a rate of substitution of one amino acid per 7.3 million years is obtained. Cladistically man, chimpanzee and gorilla are equally distant. Thus, the one alpha substitution in the gorilla lineage indicates a time of separation of the three forms on the order of 0 - 3.7 million years ago. The African apes and man have approximately 5 to 6 alpha chain substitutional differences from *M. Mulatta* and *M. fuscata*. With six differences a total of 42 million years of divergence or 21 million years per lineage would be expected which is in sound agreement with the immunologically predicted date.

Previous estimates of the rate of evolution of haemoglobin are about one substitution per 3.5 million years (Dickerson 1971). If man and chimpanzee diverged 15 million years ago, then it would be expected that they would differ by approximately 8 to 9 amino acid substitutions. The average Old World monkey differs by some 14 nucleotide substitutions from the African apes and man in both alpha and beta chain. This difference equates to a time of divergence of some 24.5 million years for cercopithecoids and hominoids.

An analysis of the available myoglobin data yields similar results (Romero-Herrera et al. 1973). Man and chimpanzee differ by one amino acid. The rate of substitution of myoglobin between the anthropoids and prosimians assuming 70 million years time of divergence and given an average of 21 amino acid differences between the two taxa is 6.6 million years per substitution or 3.3 million years per two lineages. Since man and chimpanzee differ by one substitution, this gives a best estimate from 0 - 3.3 million years for their divergence. A time of separation of 15 million years for these forms would lead us to expect between 4 and 5 substitutions. Man and Chimpanzee differ from the Old World monkeys by an average 6.5 substitutions. This predicts a divergence time estimate of 21.5 million years given a rate of 1 substitution per 6.6 million years.

The sequence data are all concordant in showing that man and chimpanzee are extremely closely related at the protein level. Out of the 430 amino acids sequences from alpha and beta haemoglobin, myoglobin, and fibrinopeptides, man and chimpanzee differ by only one substitution. The calculation of an absolute time of divergence of man and chimpanzee based on such small sequence difference is of course statistically invalid. There is in all probability no difference between 0,1, and 2 substitutions when 1 is expected; however, the range of dates predicted by the small sequence differences is all in the direction of much less than 15 million years. In fact, using the assumption of a divergence date of 15 million years and the rates of evolution of the molecule, yields an expected number of substitutions far greater than what is actually found. In contrast, where enough data is available for analysis, the date of the cercopithecoid-hominoid divergence using the acutal sequence difference given the calculated rate of evolution of the molecule, is very close to what the immunological data would predict.

Three other immunological studies have some relevance. The first is the composite immunological studies of Goodman (Goodman _et al_. 1971, 1973) Goodman has converted his antigenic distance into a relative distance (Goodman and Lasker 1973). As shown in Table 1-18 the ratio of the man-chimpanzee distance relative to the catarrhine-platyrrhine index of 1.0 is 0.12 which agrees well with an albumin ratio of 0.12 and a transferrin ratio of 0.13. Since the direct ratios agree so well a time of divergence based upon this ratio would show close agreement. The second immunological study is that of Nonno *et al*. (1969) using carbonic anhydrase B and C. With antisera prepared to purified carbonic anhydrase B from *Homo sapiens*, chimpanzee differed by 4 I.D. units, the Old World monkey average was 55 (5 species), and the New World monkey average of 3 species was 84. Values very similar to these are obtained with anti-*Homo sapiens* transferrin. Again the data indicates the close genetic similarity of man and chimpanzee.

A third immunological study is that of Hanke *et al*. (1973). Rabbit antisera were directed to the purified lysozyme from human and baboon. With the antisera prepared to the lysozyme of *Homo sapiens* the lysozyme of *Pan* shows no difference while *Gorilla* is 32 units distant. However, the lysozyme of *Pongo* is virtually indistinguishable from that of human. The six Old World monkey species tested differed by an average of 120 immunological distance units. The three New World monkeys differed by an average of 133 units. From a baboon perspective, human and chimpanzee differ by 66 units, while gorilla is 38 units, and orang is 76 units distant. The three New World forms are an average of 36 untis distant from baboon. The results of reciprocal tests are not in close agreement as with anti-human lysozyme, baboon is 127, and human is 66 with the reciprocal anti-baboon lysozyme measurement.

The close genetic relationship of man and chimpanzee is emphasized by the lack of differences between the lysozymes of these two forms as measured by micro-complement fixation. Yet, the gorilla lysozyme differs from that of human by 32 units which represents approximately 6% sequence difference (Hanke et al. 1973). This difference, if it is real, is the largest sequence difference detected between the proteins of man and the African apes. There is some question whether this difference may be an immunological artifact and not a real sequence difference. For example, from the baboon perspective, the gorilla is 28 units less distant than either chimpanzee or human. Thus, it is unclear whether there is an actual sequence difference of this magnitude or whether the difference is due to the imperfect correlation of immunological difference and sequence difference.

It has become possible to measure genetic difference by nucleic acid hybridization, and data are now available on several primate species (Kohne 1970; Kohne et al. 1972; Hoyer et al. 1972). Using "nonrepeated" DNA sequences, Kohne has estimated that human-chimpanzee hybrid DNA dissociates at a temperature of 1.5°C lower than the dissociation temperature of reannealed native human DNA (Kohne 1970; Kohne et al. 1972).

On the other hand, Hoyer (Hoyer et al. 1972) has estimated that the difference in dissociation is 0.7°C for human and chimpanzee. The absolute values of Δ Tm of man and chimpanzee are certainly different. However, what is important is the relative differences. If a human-capuchin difference of 10.5°C is taken as representative of a platyrrhine-catarrhine distance and 35 million years is used as the time of separation of the two infraorders, a human-chimpanzee difference of 1.5°C translates to a 5 million years divergence time. Similarly a difference of 6.3°C between human and green monkey translates to a time of separation of 21 million years. The human-gibbon differences of 3.5°C translates to a divergence estimate of 11.7 million years. All are in excellent agreement with the time of divergence calculated using the immunological data.

The additional data provided by Hoyer (Hoyer et al. 1972) provides us with cladisitc information, as a second reference point is provided. Radioactive orang DNA is used in the comparisons along with the radioactive human DNA. The data suggest that from an orang perspective the gibbon is as far removed as are the African apes and man. Secondly, gorilla, chimpanzee and human seem to form a unit with somewhat more evolution occurring along the gorilla lineage. From a human perspective, the human-chimpanzee-gorilla distance is 0.18 of the human-green monkey distance (1.05°C vs. 5.7°C). This works out to a time estimate of 3.5 million years if 20 million years is used for the cercopithecoid-hominoid divergence. Similar analysis show the Homo vs. Pongo vs. Hylobates divergence to have occurred 10 million years ago. From a radioactive orang DNA perspective the human-chimpanzee-gorilla vs. orang distance is 2.0°C compared to a green monkey-orang difference of 4.3°. This yields a divergence time estimate for human and orang of 9.3 million years again assuming a hominoid-cercopithecoid separation time of 20 million years.

Table 1-25 shows a summarized statement of what various macromolecules reveal of the genetic and temporal relationships of man and chimpanzee. The most valid estimates for times of separation are those found for the hominoid-cercopithecoid and Homo-Hylobates divergences. These forms have had enough evolutionary time separating them so that their macromolecules have evolved sufficiently to give valid estimates of genetic distances. The text details how well these estimates from various macromolecules agree as to the times of divergence.

The man-chimpanzee genetic distance is much smaller than either the

TABLE 1-25

Comparison of the Differences Found Between Man and Chimp in Their Macromolecules.

Dates of divergence are calculated on the basis of rates of evolution found for that specific molecule within the primates.

Source of Data	Observed Difference between Man and Chimp	Expected Difference Assuming 15 M.Y. Separation of Man and Chimp	Time of Divergence of Man and Chimp X 10^6 yrs.
Fibrinopeptide[a]	0	7	0 - 10.5
Haemoglobin[b]	0	8-9	0 - 3.7
Myoglobin[c]	1	4-5	0 - 3.3
DNA (Kohne)[d]	1.5° C	4.5° C	5.0
DNA (Hoyer)[e]	0.7° C	4.3° C	2.5

---

[a] Data from Wooding _et_ _al_. (1972).

[b] Data from Goodman _et_ _al_. (1971).

[c] Data from Romero-Herrera _et_ _al_. (1973).

[d] Data from Kohne _et_ _al_. (1972)

[e] Data from Hoyer _et_ _al_. (1972) If an average of the distance from human to chimp and gorilla is used, then the divergence time estimate increases to 3.5 M.Y.

Homo-Hylobates or the hominoid-cercopithecoid difference. With such small numbers seen in the sequences, a valid statistical estimate of the time of separation is impossible. Enough sequence data are available to estimate an average rate of substitution for each molecule within the primates. Once this is determined it can be calculated what would be expected if a longer divergence time for human and chimpanzee were in fact true. Upon analyzing the sequence and nucleic acid hybridization data for average evolutionary rates found within the primates, it is found that the data are consistent in indicating that the actual amount of time separating man and chimpanzee or gorilla is small. Enough of a difference has accumulated between the hominoids and the cercopithecoids to indicate that the *Homo-Hylobates* distance is on the order of 10 million years.

Without access to other sources of information, a range of from 0 to 10 million years with a mean of 4 to 5 million years is the best estimate that can be made of the time of separation of the African apes and man based upon their macromolecular differences. This is not to say that there is an equal probability of this divergence event occurring at any point within this range. Each additional source of macromolecular evidence, because of their close agreement in their estimation of the time of separation of man from the African apes increases the height of the distribution curve that describes the probability vs time plot. This additional data increases the probability that the actual time of divergence is in the range of 4 to 8 M.Y. The range narrows as the standard diviation of the distribution drops. The total macromolecular picture suggests then that the maximum probability for this divergence is from 4 to 8 M.Y. The probability rapidly slopes to zero on either side of this maximum probability estimate.

An additional source of data, that from fossils, may further narrow this range so that even stronger conclusions may be drawn in estimating times of separation of these taxa. Various hominid remains have been recovered from dateable East and South African Plio-Pleistocene deposits. Leakey (1973) has ascribed over 100 fossil specimens from East Rudolph, Kenya to at least two different genera of hominids, Australopithecus and Homo. These fossils date from 3 to 1 million years. Similarly in the lower Omo basin of Ethiopia, Howell (Howell 1969; Howell and Coppens 1974) has recovered hominid remains from two main localities dating from 3 to 1.4 million years. Unquestioned hominid remains have also been discovered in South African deposits of unknown absolute dates; but these forms are certainly within the range of time of similar forms in East Africa (Howell 1967; Brain 1972). Earlier fossil specimens have be considered to be hominids, for example Ramapithecus (Simons 1969, 1972; Pilbeam 1966; Leakey 1969). However, the status of Ramapithecus as a hominid has been questioned on morphological grounds (Walker and Andrews 1973). The presence of an hominid in the fossil record before approximately 4 M.Y. remains to be demonstrated.

The range of time estimated for the divergence of man and the African apes based solely on differences in their macromolecules must be shortened in one direction as a result of paleontological evidence. The minimum time for this divergence using dates from deposits containing hominids cannot postdate 3 to 4 M.Y. On the opposite end, macromolecular comparisons restrict the maximum divergence time to approximately 10 M.Y. However, the weight of macromolecular evidence strongly suggests that the separation of the lineages leading to Homo and Pan is nearer the recent end of this restricted range. It becomes increasingly difficult to reconcile a divergence time of man and the African apes of much more than 5 M.Y. with the growing body of molecular information and the remaining scarcity of suitable candidates for hominid ancestry that predate this time.

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II. THE FOSSIL EVIDENCE FOR HUMAN EVOLUTION

AREA I.

South Africa
Sterkfontein
Swartkrans
Kromdraai
Makapansgat Limeworks Deposit
Taungs

SOUTH AFRICA

History of the Discoveries and Early Geomorphologic Investigations

Fossiliferous hominid-yielding sites at Sterkfontein, Swartkrans and Kromdraai are all grouped within the Blaaubank River Valley approximately six miles north of Krugersdorp, Transvaal, Union of South Africa. (Figure 11-1) The Makapansgat Limeworks deposit is located about ten miles to the northeast of Potgietersrust in the central Transvaal.

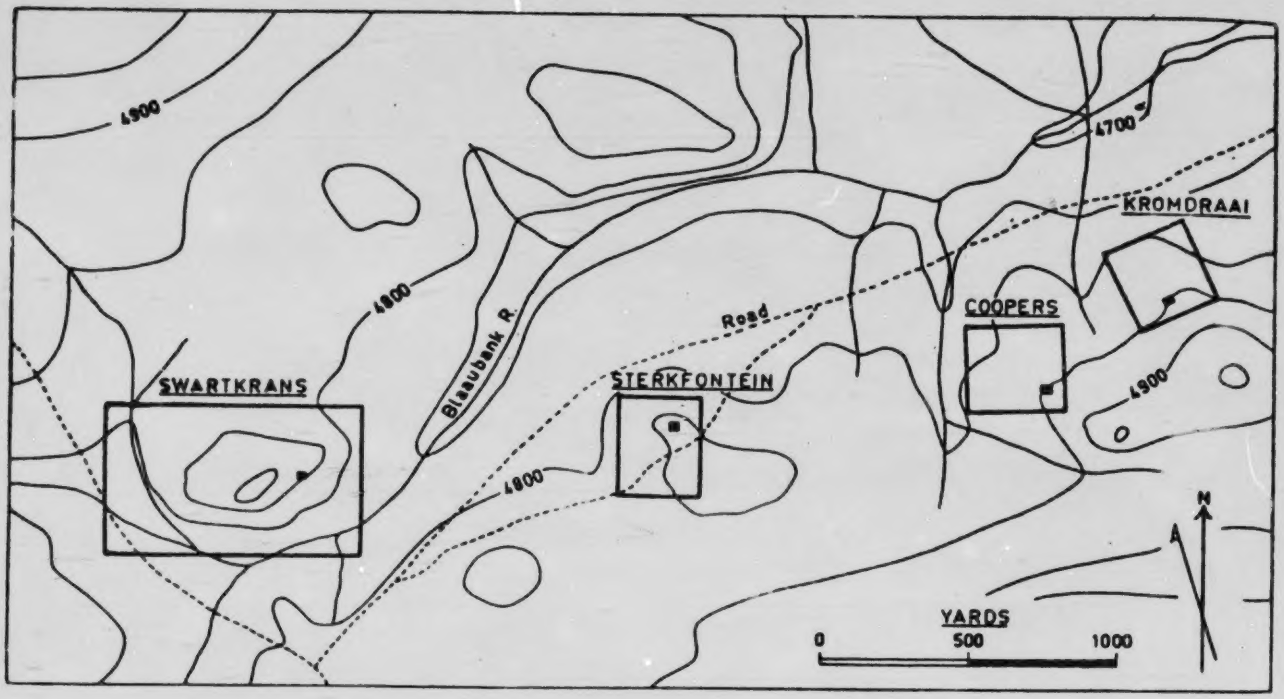
STERKFONTEIN

During 1936 Robert Broom was notified of a cave at Sterkfontein which had yielded a fossil assemblage similar to the one he had previously collected from a nearby cave site. With the help of the limeworks manager Broom recovered from the deposits the skulls of three baboons, a sabertooth cat and an endocast of the brain of an australopithecine. Later search revealed numerous parts of the skull itself which he later named Plesianthropus transvaalensis. Several other hominid specimens were subsequently recovered from the upper part of the deposit, but it was not until 1937 that specimens came to light from a horizon some 10 meters beneath the initially discovered deposit. In 1938 at Kromdraai, Broom discovered a new hominid form which he named Paranthropus, and he abandoned his excavations at Sterkfontein until 1946. On April 18th of 1946 the most complete cranium was unearthed (STS 5) and was nicknamed "Mrs. Ples". Soon after this discovery the site was visited by Professor Lombard, a geologist, who initially described the cave fillings as consisting of a uniform stratigraphical sequence. Broom continued to extract specimens until January, 1949, when he began work at Swartkrans.

During 1956, C. K. Brain, with the urgings of John Robinson, recovered numerous stone artifacts in loose breccia lying near the surface near a small

Figure II-1

Fossil Hominid Bearing Cave Sites in South Africa

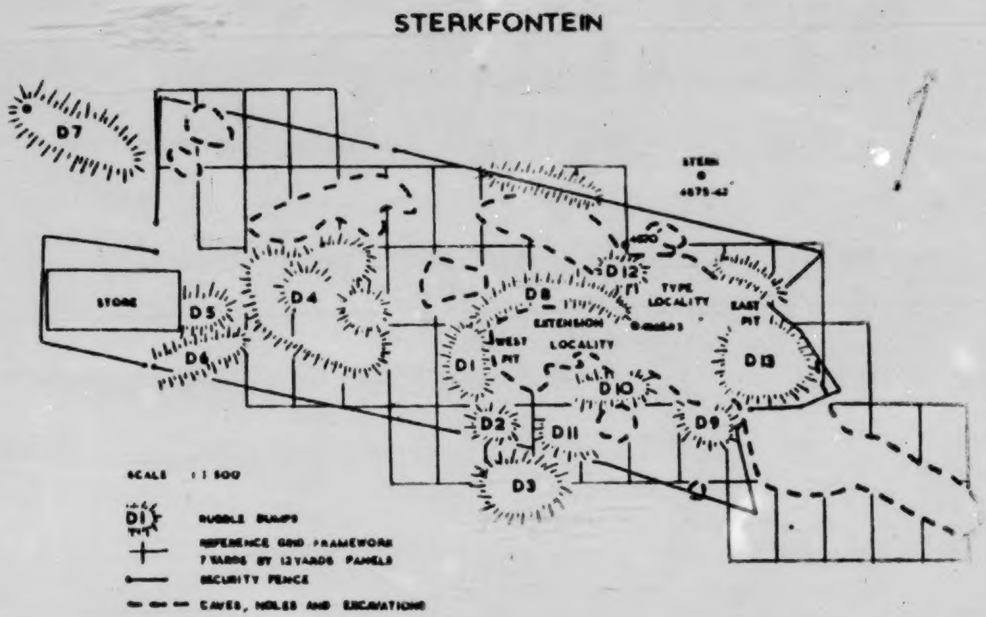

4900
4700
KROMDRAAI
4800
Road
COOPERS
Blaaubank R.
SWARTKRANS
STERKFONTEIN
4900
4800
N
YARDS
0
500
1000

From Brain, Trans. Mus. Mem. 11 (1958): 54.

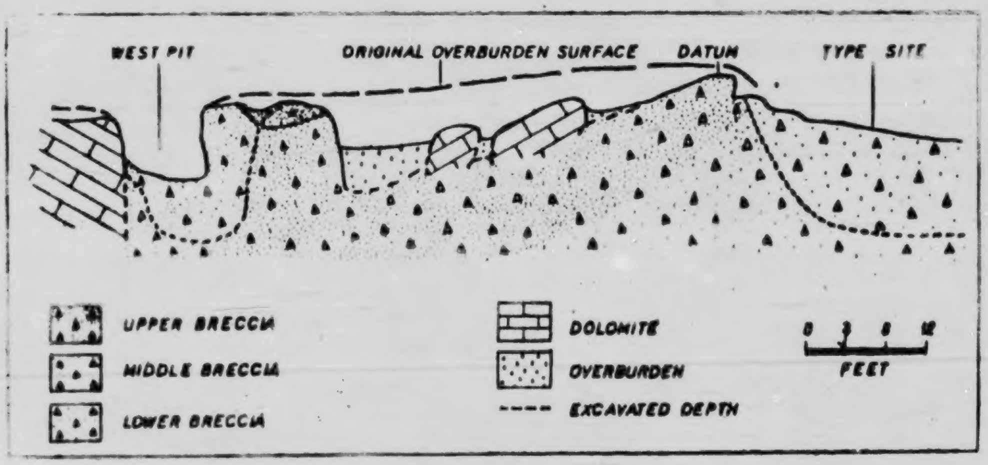
pit west of the type site. Further excavations were undertaken by R. Mason and Brain who stripped off the overburden between the two sites and demonstrated that the breccia of the West Pit was laterally continuous with that of the upper type site but that the two were probably separated by some temporal disconformity (Robinson and Mason, 1957). During the field investigations of 1957, Mason, Brain and Robinson excavated additional artifacts of the South African Middle Stone Age from refilled breccia which overlay older deposits. However, during the same year, a volume of West Pit (= Sterkfontein Extension Site) breccia excavated by Robinson, revealed a series of technological artifacts and several teeth of what was described as Australopithecus, demonstrating the association between the hominid remains and the stone tools. These artifacts were classified by Mason as Late Olduwan. No stone tools, however, have been found in association with Australopithecus at the type site (STS).

The Sterkfontein cave deposits at the type site have not been completely exposed, and as a consequence, the extent of the deposition is not completely known. Stratigraphical investigations were undertaken by Brain (1958) who showed that the plan of the cave was long and hall-like with a length of about 55 meters (Figure 11-2). The roof is only partly eroded and is preserved in area somewhat less than half the width of the cave. Abutting on the west wall of the type site and extending due west from it for 60 feet is the extension site. The original cave entrance was probably long and narrow and extremely precipitous, barring easy entrance to most animals. As a result, most of the hominid remains come only from the uppermost levels of the cave filling immediately underneath the dolomite roof which accumulated after the front portion of the cavern had been filled. Brain's original plan view of the Sterkfontein cave was criticized by Robinson (1962) who

Figure 11-2


STERKFONTEIN
D7
STORE
D5
D4
D6
D8
D12
TYPE LOCALITY
EXTENSION
EAST PIT
WEST PIT
LOCALITY
D1
D2
D3
D9
D10
D11
D13
SCALE 1:500
D1
RUBBLE DUMPS
REFERENCE GRID FRAMEWORK
7 YARDS BY 12 YARDS PANELS
SECURITY FENCE
CAVES, HOLES AND EXCAVATIONS

Plan of the Sterkfontein site (from Tobias and Hughes 1969: 164)


WEST PIT
ORIGINAL OVERBURDEN SURFACE
DATUM
TYPE SITE
UPPER BRECCIA
MIDDLE BRECCIA
LOWER BRECCIA
DOLOMITE
OVERBURDEN
EXCAVATED DEPTH
0 3 6 12
FEET

East west section through the West Pit and part of the Type Site

(from Robinson 1962: 97)

claimed that the west wall should run approximately 18° westward from the angle shown. Likewise, the original opening was probably on the higher southern side of the cavern which was further demonstrated by the fact that traces of stratification ran from a southern high point to a northern low point (Robinson 1962: 93).

During two seasons of excavation in 1957-58 the extension site was investigated and a detailed map was drawn. The primary purpose of the excavation was to determine whether the stone industry earlier reported by Brain occurred in any breccia in situ and to determine the relationship between the stone tool industry and the australopithecine fossils.

This excavation yielded some hominid fossil material including a fragment of a maxilla of a child and several isolated teeth as well as stone tools, and according to Robinson (1962: 95) this demonstrated for the first time "the synchronous presence of an australopithecine and a stone industry in the same site". Robinson, however, showed that the breccia in the extension site was younger than that of the type site and went on to define three distinct breccias present at Sterkfontein. The Lower Breccia, earlier referred to as the "Pink Breccia" of the type site is the oldest breccia associated with almost the entire collection of australopithecine fossils. Though it is not exposed in the extension site except for a few blocks in the West Pit area, it completely filled the type site cavern.

The Middle Breccia or artifact-bearing breccia rests uncomfortably on the Lower Breccia. Middle Breccia fillings must have occurred after collapse rather than erosion of the Lower Breccia in the extension site area. It was exposed in the extension site and in the upper portion of the west wall of the type site and is the sole source of the stone tool industry. The reported maximum depth is some twenty feet.

The Upper Breccia or the dark-brown breccia is the youngest of the cave breccias and is found in a restricted area near the north wall of the West Pit. As yet, no hominid material has been recovered from these sediments.

Robinson (1962) refutes a claim once made by Louis Leakey that the Middle Breccia hominid is more closely allied to "Telanthropus" from Swartkrans by demonstrating that in various tooth dimensions the lower and middle hominids are equivalent. However, Mason (1962: 123) disagreed and believed that the Sterkfontein tool-maker was a hominid of the pithecanthropine grade.

Robinson shows that because the artifacts of the Middle Breccia were scattered uniformly throughout the deposit that one was not dealing with a local concentration; a result of a single restricted episode of artifact manufacture. Rather the number of artifacts found in the Middle Breccia were a reflection of the "tool-making activity in the neighborhood over a significant period of time" and that the absence of tools in the Lower Breccia was probably due to the fact "that there were no tool-makers about at the (earlier) time" . (Robinson 1962: 104)

During 1964 and 1965 plans were again drawn up for further systematic excavations at Sterkfontein. The archeological excavations were designed to remove the extensive overburden in order to determine the relationship of the various breccia outcrops and caverns, and to map the extent of the cave system and the original entrance. Tobias and Hughes (1969) believed that the cavern system was much more extensive than that exposed up to 1956 and reported by Robinson (1962). Further exposures of breccia were discovered to the west of the West Pit (formerly the extension site). The old west wall described by Robinson was determined to be a collapsed portion of the cave roof and the excavations to that date had not yielded further evidence of a true western wall. Attempts at relocating the original deposits of one of the Sterkfontein hominids, STS 5, showed that the skull appears to have been situated above a band of travertine possibly continuous with a large exposure on the west wall of the type locality. In that location the travertine lies above what has been considered to be the "Lower Breccia" and is in fact the base of the "Middle Breccia" (Tobias and Hughes 1969: 164). This led Brain to question whether any of the hominids belonged to the "Lower Breccia", and Brink to suggest that the "Lower Breccia" may not have been a cave breccia at all but a fault breccia which antedated the formation of the original solution cavern.

Roughly 17,000 macromammalian fossilized bones and over 100,000 micromammalian remains were recovered in the 1968-69 season. Within these fossils one isolated M_1 and other more fragmentary hominid molars were reported. Attempts at absolute dates for the deposits using a number of different techniques failed to yield any significant results (Tobias and Hughes 1969: 165-66).

In August, 1976, a new fossil skull was reported by Hughes and Tobias (1977). The skull according to the authors resembled Homo habilis from Olduvai Gorge in the comparable parts and was derived from what has now become known as Member 5 of the Sterkfontein Formation. The fossil was uncovered near the area which Brain and Robinson in 1958 had recovered the first stone tools in the West Pit. Member 5(formerly the "Middle Breccia") is separated from Member 4 by perhaps as much as 0.5 - 1.0 million years according to Vrba's study of the fossil bovidae (Vrba 1975). Until the announcement of this fossil skull, which consists of most of the bones of the cranium, Member 5 yielded only a few teeth and jaw fragments of the fossil hominids of that time. These authors believe that this new specimen, Stw 53, strengthens the view that A. africanus was earlier in time than early Homo and is the most likely claimant to have been ancestral to Homo habilis.

KROMDRAAI

Excavations of this cave began in 1938 when Robert Broom obtained the first hominid fragment which consisted of a palate and an in situ molar tooth This specimen was obtained from the manager of the limeworks at Sterkfontein who himself had received the specimen from a local schoolboy. Further investigations led Broom to a nearby hill about a half mile from Sterkfontein. Additional specimens were recovered which belonged to a nearly complete cranium lacking only some of the upper teeth. Broom designated the reconstructed skull (TM 1517) as the type specimen of a new genus and species Paranthropus robustus.

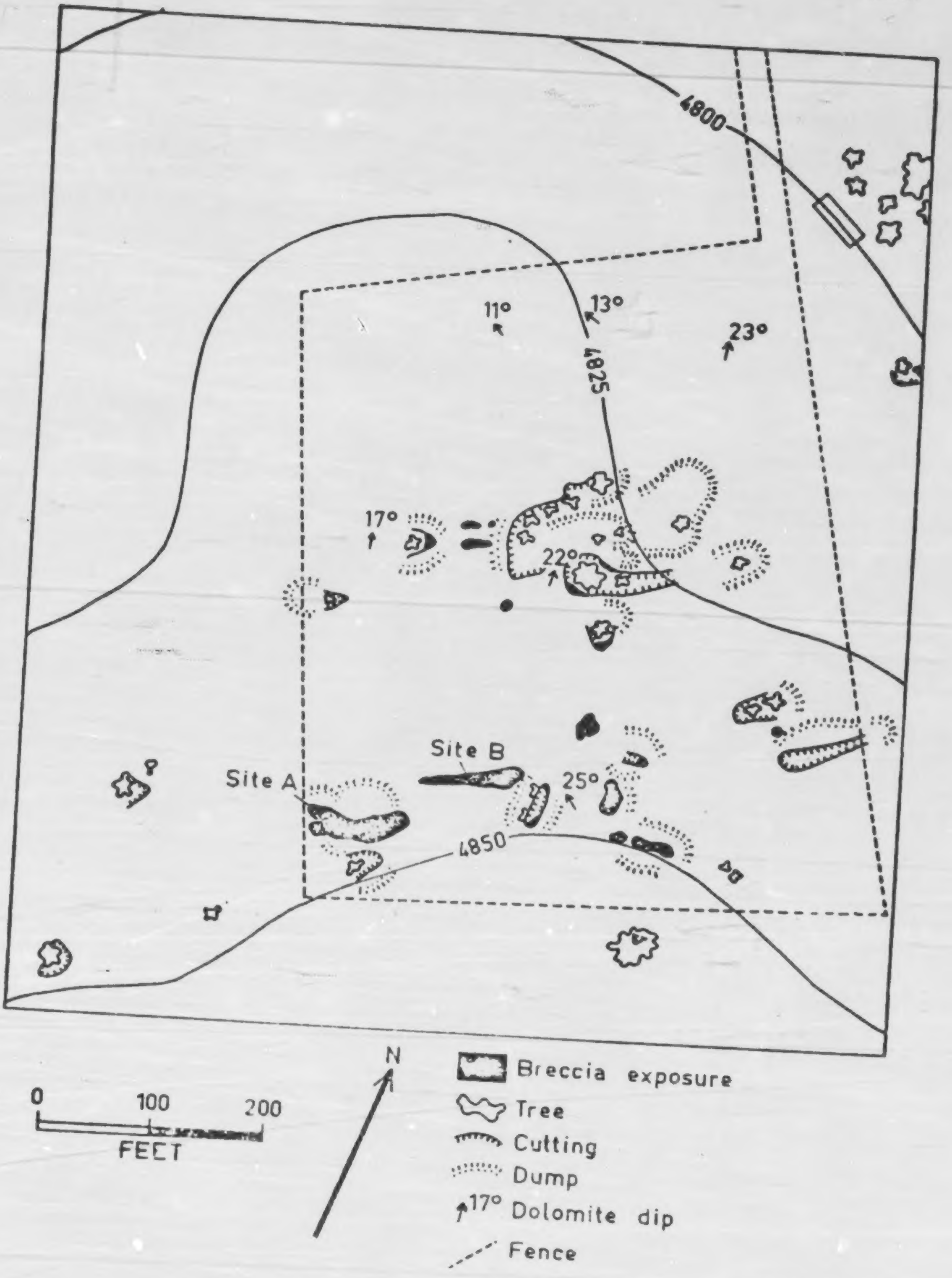
Further investigations at Kromdraai were delayed until 1941. Excavations at that time exposed an adolescent mandible with nearly complete milk dentition. Work was again halted until March, 1955, when discoveries by C. K. Brain increased the number of hominid fossils by unearthing additional isolated teeth and large numbers of fragmentary bone. In addition to the australopithecine-bearing deposit designated Kromdraai B, another breccia-filled fissure occurs on the Kromdraai hillside. This is the faunal site, or Kromdraai A, which produced the abundant fossil animal remains, though no hominid specimens, during the excavation of Broom in 1947. It had become customary to associate the faunal remains from Kromdraai A with the hominid specimens from B and to assume contemporaneity though the recent evidence suggests this assumption to be incorrect. The australopithecine site was reinvestigated in 1955 by Brain who concluded that the soil consisted of decalcified breccia which had weathered in place through the action of rainwater. In the course of the excavation Paranthropus remains were found in the upper two feet only, suggesting that the upper parts of the deposit accumulated at a time when australopithecines inhabited the area.

The two sites, Kromdraai A and B, are both elongated but relatively narrow. At Site A, the dolomite roof has been totally eroded and only part of the roof remains at Site B. The cave was filled to the roof with breccia embedding the stalactites. The breccia in the cave could be divided into two types: the coarse-grained stony breccia which was deposited at the eastern end of the site and the remaining finer-grained stratified material. The original cave entrance was no doubt directly above the eastern end of the cave, for the surface-derived material which washed into the cave was naturally sorted with the heavier stony fraction remaining below the entrance and the finer material carried further into the cavern. (Figure 11-3)

SWARTKRANS

Towards the end of 1948, excavations began at a nearby locality at Swartkrans. The first specimens to be recovered were isolated teeth and parts of a large mandible of a new hominid species which was named *Paranthropus crassidens* (Broom 1949). During April, 1949, a mandible fragment of another new hominid species was described as *Telanthropus capensis*. Excavations continued throughout 1949 but were halted at that time by the commercial quarrying ventures on the site who continued their operations until 1952. The Swartkrans cave was abandoned until April, 1965, when Brain began excavations of undisturbed breccia where a representative sample of over 14,000 bone fragments was recovered. These investigations further showed the existence of still older breccias occupying the eastern extension of the site. King (1951) first mentioned the geology of the Swartkrans site as being similar to the sequence he had described from Makapansgat. The two deposits of red sand were assumed deposited during arid conditions while the intervening "Main dripstone" was laid down duringa period of increased rainfall. The recovered australopithecine remains from all the various known

Figure II- 3


4800
4825
4850
11°
13°
23°
17°
22°
25°
Site A
Site B
N
0
100
200
FEET
Breccia exposure
Tree
Cutting
Dump
17° Dolomite dip
Fence

MAP OF KROMDRAAI DEPOSIT.
Brain, Trans. Mus. Mem. 11 (1958): 91.

sites were thought to belong to the "Older red sand", and therefore broadly contemporaneous. The geomorphic evolution of the Swartkrans caves has involved cavern enlargement by solution and roof collapse, accumulation of flowstone and dripstone, and fillings by soil and detritus with renewed corrosion and erosion of the earlier fills.

Robinson (1952a) provided the initial detailed description of the site and its deposits as they were exposed at that time. He demonstrated that the "main dripstone" lay in direct contact with the dolomite floor with no evidence of any earlier deposits appearing. Thus King's "Older red sand" layer was not present at Swartkrans. Brain and Robinson (1953) showed that the cave breccia was stratified and probably laid down in water. Brain (1958) expanded on Robinson's original site report and described the Outer, Inner and Lower cave unit showing how they had formed around the "floor block" which had collapsed from the roof of the original solution cavern. This floor block was previously covered by the "main dripstone" layer which sealed off the Inner from the Outer cave. The Outer cave was subsequently opened to the surface and filled with the so-called "Pink breccia", the source deposit of the australopithecine fossils. Later, with a reduction in the height of the floor block, the Inner cave was opened and filled with what became known as the "stratified brown breccia" which is separated from the "Pink breccia" by a marked unconformity. Hillside erosion ultimately removed the roof from the Outer cave exposing the fossiliferous breccia to the outside. The Lower cave was opened by Brain in 1973 and was subsequently shown to be a cavity through which water passed from the surface to lower subterranean reservoirs. Water passing through the Outer cave dissolved channels in the existing "Pink breccia" and carved a series of irregular channels some of which later became refilled with calcified channel fill. The *Homo* mandible

SK 15 (= Telanthropus) was probably derived from this sort of deposit rather than from the main Paranthropus-bearing breccia suggested by Robinson (1953).

Recurrent problems persisted, however, in understanding the distribution of fossils within the Outer cave filling. The primary difficulty arose in the interpretation of the bovid remains studied by Vrba (1975), who concluded that the remains consisted of a mixed assemblage of two different ages. The older assemblage contains the remains of the robust australopithecines and the "SKa" fauna; the "SKb" fauna is more recent. However, the majority of bovid specimens come from the Outer cave which was previously thought only to contain the older Pink breccia and associated channel fills. It was unlikely that the entire recent bovid fossils come solely from the more recently deposited channel fills. With the most recent reinterpretations of the Swartkrans stratigraphy it is apparent that the younger deposits of the "stratified brown breccia" is also well represented in the Outer cave especially near the point of entry into the cave. Butzer (1976) has recently redefined the older and younger breccias as Members 1 and 2 of the Swartkrans Formation. The Inner cave facies of Member 2 represent a filtered sorted variant of the Outer cave, lacking the most coarse fraction which was trapped in the Outer cave. Within the Member 2 deposits, Vrba (1976) has described earlier and later "SKb" assemblages - the earlier group being derived from solid Member 2 breccia and the later group from subsequent channel fills of various ages. All of the remains of approximately 88 Paranthropus individuals as well as the single Homo composite SK 846/847/80 belong to the Member 1 breccia, while the second Homo SK 15 belongs to Member 2 deposits. The incidence of hominids and cercopithecoids is sharply reduced from Member 1 to Member 2 while the percentage of predated bovids increased from 24% to 62%. Apparently the robust australopithecines disappeared in the interim between the accumulation periods of Member 1 and Member 2. The most recent interpretation of the external appearance of the Swartkrans sequence suggests predominantly open grassland or parkland environment with effective moisture perhaps slightly greater than that of today during the accumulation of at least some of the units of Members 1 and 2 (Butzer, 1976).

Age of the Swartkrans Formation

The Swartkrans Formation consists of two and perhaps three major members. (Table II-1) With the absence of absolute dates, age estimations remain speculative. Although recent paleomagnetic determinations (Brock *et al*., 1977) proved inconclusive, Vrba (1975), based on the bovid remains, has suggested that the "SKa" fauna belongs to the Swartkrans faunal span which indicates an age of approximately 2 - 1.5 m.y. Fossil taxa represented in Member 1 consists of 64% extinct forms (23 out of 36). Member 2 and channel-free sediments can probably be regarded as covering a time from the Cornelia span almost to the present day. The earlier "SKb" fauna of Vrba from Member 2 is perhaps 1.0 m.y., equivalent to mid-Pleistocene site of Elandsfontein, while the younger unit, more recent than Member 2 deposits (= Vrba's later SKb fauna) is probably of upper Pleistocene age (Klein, 1977). Of the forty taxa represented in Member 2 breccia, only 13 (33%) are extinct (Brain, 1976).

Table II-1

Lithostratigraphy and biostratigraphic
correlations at Swartkrans
(Butzer, 1977)

Younger fissure and cavern fills		Late SKb fauna "Upper Pleistocene"
Swartkrans Fm		
Member 2		Early SKb fauna "Middle Pleistocene"
Member 1		
Bed C	Five detritus	SKa fauna
Bed B2	Coarse detritus	"Lower Pleistocene"
Bed B1	Coarse detritus Collapsed breccia Abrupt transition marking the point where the cave was first opened to the surface hillside.	
Bed A	Travertine on bedrock Residual grey breccia of Brain (1958)	

Associated Archaeological Remains

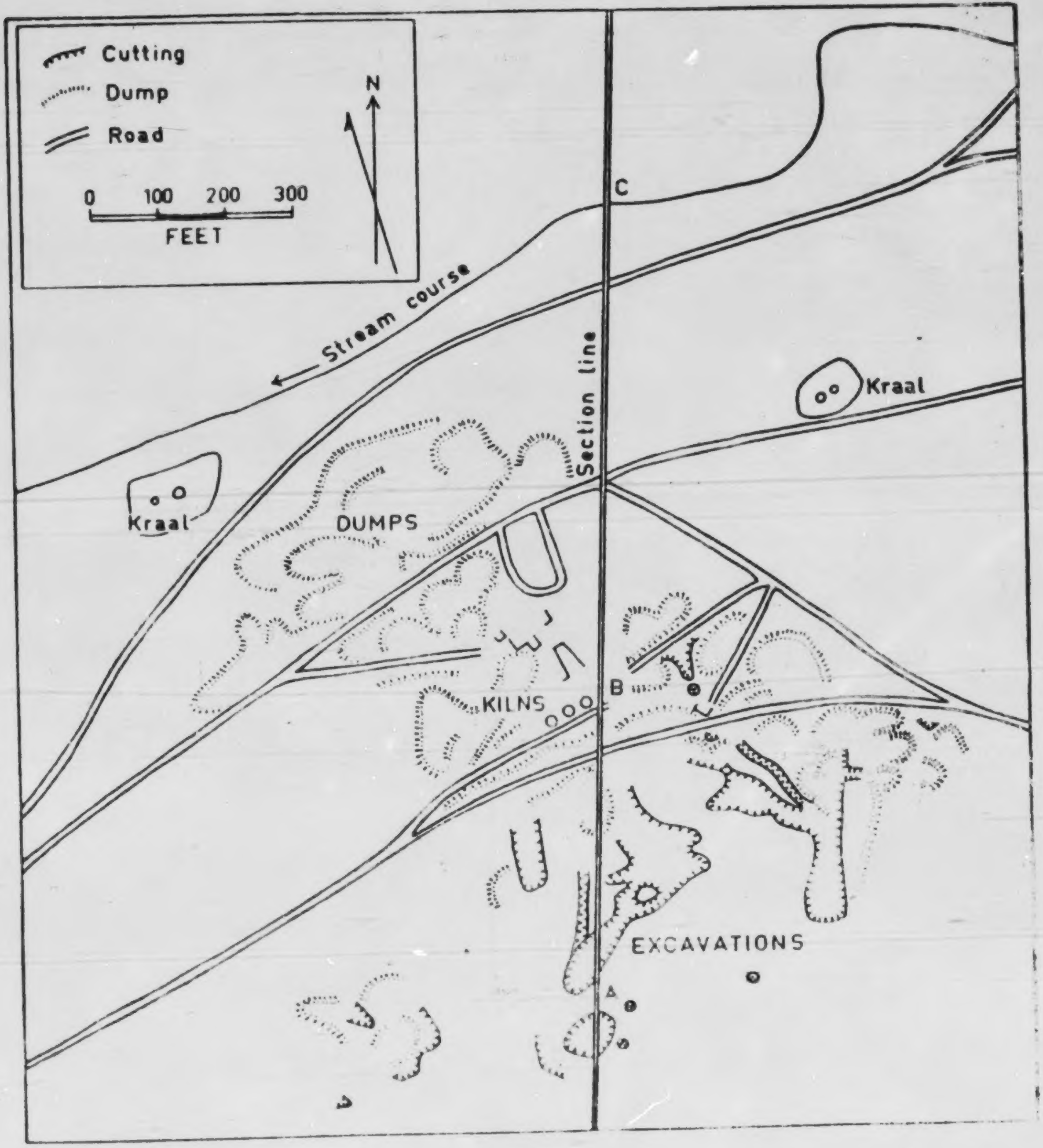
Stone artifacts from the fossil-bearing breccia of the Outer cave are not abundant: so far only 35 specimens have been recovered and described (M. Leakey, 1970). All were recovered as the result of mining operations and lack stratigraphic correlations. Only one tool, SK 3963, a heavy-duty scraper, can be assuredly associated with the older Member 1 breccia. All of the other tools probably come from the more recent deposits (Brain, 1976).

MAKAPANSGAT

The Limework's cave is situated on the Makapansgat Farm some 150 miles to the northeast of the Krugersdorp. (Figure II-4) The earliest reference to the site was made by Dart (1925) when he described a very fragmented and largely unidentifiable bone assemblage sent him by W. Eitzman, a visitor to the site. Much of the assemblage had been blackened as if burnt and Dart's conclusions were that the hominids had been responsible for the bone accumulation. In 1947, the first human remains were discovered, consisting of a fragmented occipital. Within a year, however, additional hominid material, including an adolescent male mandible, cranial fragments, teeth and an adolescent pelvis, were recovered together with an extensive associated fauna from the Limework's dump. Because Dart believed that the hominid remains were of those individuals who had been responsible for the burnt bones, a new species of hominid, Australopithecus prometheus, was created.

During the middle 1950's, additional hominid remains were recovered along with a collection of several stones showing artificial fracture. It was the opinion of Brain, van Riet Lowe and Dart that the horizon which had yielded the tool culture (= Kafuan) was contemporaneous with that which had yielded the hominid remains. An additional discovery of an australopithecine maxilla in 1955 overlying the pebble-tool stratum indicated a clear association betweenthe tools and the hominids. By the end of 1958, the analysis by hand-sorting of the breccia dumps south of the kilns (Figure II-4) had been completed. Further excavations commenced in 1960 when Dart and Maguire began a recovery operation of breccia lying inside of the cavern itself. Efforts were concentrated on the "Phase 2"breccia, and of the 1,600 tons of debris and breccia sorted, 10-15% of the 22,000 fractured dolomitic and chert fragments were definitely considered to be tools. (Dart, 1965). In the following

Figure 11-4


Cutting
Dump
Road
N
0 100 200 300
FEET
Stream course
C
Section line
Kraal
Kraal
DUMPS
KILNS
B
EXCAVATIONS

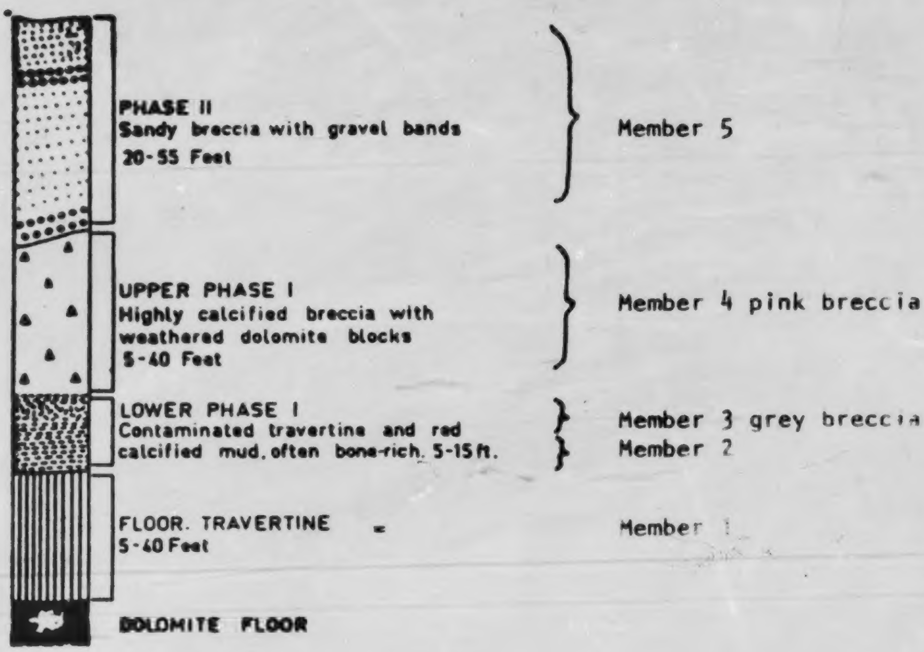
MAP OF MAKAPANSGAT LIMEWORKS DEPOSIT.
From Brain, Trans. Mus. Mem. (1958): 104.

two years Dart, Maguire and Inskeep prepared for excavations of the consolidated "Upper Phase I" breccia by beginning a trench from front to back through the entire deposit. In addition the entire surface of the cave deposit was cleared of vegetation and surface rubble, grid stanchions were erected and what became known as the "Central Excavation Area" was defined.

The majority of the Makapansgat cave roof, as at Kromdraai, has been removed by erosion exposing the consolidated breccia to the surface over a considerable area. The original cave has been described as a subsidence rather than a solutional geomorphologic feature. This interpretation required that a large solution cavern existed below the present cave and the roof of this solution cave collapsed creating a new cave above. According to Brain (1958), once the opening developed, it remained small for a considerable period of time which would account for the earlier Phase I deposits of contaminated travertines and calcified muds. A sudden enlargement of the opening initiated the apparently rapid accumulation of the Phase II deposits which, except for the southwest rear corner of the cave (= "central collapsed area"), were subsequently eroded. Continual instability of the basal dolomite floor is evidenced by the presence of large cracks which lend further evidence supporting the hypothesis of the existence of a lower cavern. (Figure II-4).

Figure 11-5

Comparative stratigraphy of the Makapansgat L.D.
(Brain 1958: 107 and Partridge 1977)


PHASE II
Sandy breccia with gravel bands
20-55 Feet
Member 5
UPPER PHASE I
Highly calcified breccia with
weathered dolomite blocks
5-40 Feet
Member 4 pink breccia
LOWER PHASE I
Contaminated travertine and red
calcified mud, often bone-rich. 5-15 ft.
Member 3 grey breccia
Member 2
FLOOR. TRAVERTINE
5-40 Feet
Member 1
DOLOMITE FLOOR

Detailed mapping of the Makapansgat site was undertaken by Partridge (1977) who suggested new nomenclature for the depositional sequence (See Figure 11-5) The newly named Makapansgat Formation constitutes the cave filling of the fossil hominid-bearing site. The lowest member (Member 1) is a contaminated travertine containing bone deposited on an irregular dolomite floor. Member 2, which forms the lower part of the Lower Phase I unit, also contains bone and consists of a brownish-red, well-bedded deposit of silt which grades upwards into more coarse material. Member 3, the grey breccia of Lower Phase I, is thin, consisting of densely packed cemented bone accumulation, unconformably overlying Member 2. Member 3 contains the majority of fossiliferous remains from Makapansgat. Member 4 is a thick deposit made up of the [illegible] breccia of Upper Phase I, consisting of dolomite fragments probably derived from roof falls, and local concentrations of bone. The

Red Phase or Phase II Breccia was renamed Member 5 and constitutes a well stratified brownish-red silty sand matrix resting unconformably upon the eroded surface of Member 4.

Most of the remains of A. africanus were recovered from Member 3 except for the posterior part of a cranium (Member 4) and a single maxillary fragment (Member 5).

Recent paleomagnetic determinations were taken by Brock et al (1977), and the results showed magnetic reversal for the samples collected from Member 1. Member 2 samples range from intermediate in the lowest deposits to normal polarity from the remaining upper samples. Member 3 was not sampled due to the physical properties of the rock itself. Member 4 lower deposits showed an intermediate horizon followed by two reversed horizons and again, in the uppermost deposits, two intermediate horizons. The placement of these polarity changes within the polarity time scale depends heavily on other evidence indicating the approximate age of the deposits. Partridge (1973), on geomorphological grounds using estimates of nickpoint migration and valley widening, calculated an age for the cave opening at 3.7 m.y., the maximum age for the deposits. Cooke (1970) using fauna evidence of fossil suids suggested an age in the vicinity of 2.5 to 3.0 m.y. White and Harris (in press) in comparing the Makapansgat suid fauna to that found at the Omo site suggest an equivalence with Members B-C of the Shungura Formation. The published formal evidence therefore suggests an age between 2.5 and 3.0 m.y. for Member 3, setting an approximateyounger limit for the age of Member 2 in which the polarity change occurs. Thus Member 2 should lie within the Gauss normal epoch and has a maximum age of between 2.8 to 3.3 m.y. while the reveresed or intermediate directions high in Member 5 may be associated with either the Reunion or the Olduvai events.

Archaeology and associated remains.

The oldest possible stone artifacts at Makapansgat were recovered from Phase II breccia by Brain, van Riet Lowe and Dart in 1954. The "Lower Phase I" breccia at the base of the deposit forms the most productive bone-bearing stratum and has yielded the majority of the bone tools described by Dart (1957). Reported stone objects occurring in the Phase II deposits consisting of pebbles and boulders do not occur in intact living floors. The objects consist primarily of dolomite in addition to the rarer chert and a very small number of quartzite forms. Phase I breccia underlying this gravel horizon preserves, however, some undoubted bone artifacts which may have lain on living floors. (Mason, 1965) The question as to whether the Phase II objects were produced by artificial fracture or natural percussion was examined by Mason (1965) and he concluded, based on the analysis of some 20,000 specimens, that in broad quantitative terms the Phase II Limeworks fractured objects have more characteristics in common with naturally fractured objects than with accepted artifact series. Partridge (1965, 115) however felt that the present samples did suggest tool-making of an "extremely crude nature and unsystematized form", even though "unequivocal classification of many of the specimens as artifacts" would be hazardous at that time. Dart (1962), on the other hand, concluded that the presence of australopithecine remains throughout the deposit demonstrates that bone and stalactitic tool-making was contemporaneous with the hominid occupation of the site.

Correlation and Age of the South African Hominid Sites

Early Pliocene deposits in South Africa have been located at Langebaanweg, some 105 km north of Cape Town in the Varswater Formation. The fossil assemblage recovered there contains 75 species of mammals, all of which are extinct. Several taxa that occur in the Varswater Formation are also known from East African deposits where they have been dated radiometrically 4 - 5.0 m.y. Though faunal assemblage is very large, primate material is rare, and as yet, no fossil hominid material has been recovered. In contrast to this there are numerous carnivore remains consisting of some twenty species, and to balance that, some 27 potential prey species have also been recognized. This proportion differs markedly from that of more recent periods (for instance Elandsfontein) which reveals eleven carnivore species and 32 prey species: an approximate ration of 1 to 3, which is characteristic of these and later deposits. According to Klein (1977: 116) this change in the ratio of prey to predator may "in part be due to the arrival and subsequent evolutionary success of meat-eating hominids."

The late Pliocene - early Pleistocene cave sites in the Transvaal (Makapansgat, Sterkfontein, Swartkrans and Kromdraai), and in the northern Cape Province (Taung), contain few of the archaic genera found at Langebaanweg, leaving no doubt that these fossilferous deposits postdate those of the Varswater Formation.

Earliest attempts at assessing the age of the hominid sites in South Africa were based on analysis of the fossil faunal remains. Ewer (1955, 1956) believed that the relative ages of the sites followed the sequence of Sterkfontein and Makapansgat, both of a similar age, preceding Swartkrans and finally Kromdraai. Taung was believed to be the oldest site, though this view was criticized by Wells (1969).

To the faunal sequence dating, climatic evidence was added by Brain (1958) giving the results of sand grain angularity (porosity) determinations and the chert-quartz ratios yielding essentially the same results as the initial faunal analyses. Brain concluded from his studies that a number of climatic changes had occurred in South Africa during the Pleistocene period; a conclusion he based on several points:

(1) The shape of quartz grains found in dolomite sands tend to be more rounded in shape with average rainfall between 400-750mm, and more angular with rainfall in excess of 900mm. According to Brain, quartz components within the dolomitic rock is angular and a wetter climate dissolves out greater quantities of quartz. In drier settings weathering of the dolomite is slower so that the released grains are altered and smoothed with time In the very dry climates, the rounding process is affected by calcite cement adhering to the quartz grains.

This analysis of angularity of quartz grains has several problems however; the most difficult being that more than one environmental factor (i.e. rainfall) is responsible for reduction of the angularity of the material. weathering of quartz involves at least six factors, none of which have had the proper controls established. Certainly rainfall is one such factor, time of exposure, distance of transport, slope of transport, and the Ph of the rainfall are others which must be considered. Changes in any of these variables will have some effect on the weathering process, the exact effect has yet to be discovered experimentally.

(2) Sediment color tends to reflect the depositional environment. Hillside dolomite soils exposed to humid conditions tend to be brownish; soils exposed to more arid conditions are more reddish. From these data it was suggested [illegible] rainfall in South Africa varied considerably during the lower

Pleistocene, and that the deposits at Makapansgat and Sterkfontein were accumulated during dry conditions; those at Swartkrans and Kromdraai were accumulated during later wetter (pluvial) conditions. Such correlations suggested that the two hominid forms may have differed with respect to environmental preferences and diet.

These arguments were criticized by Butzer (1971), who claimed that the finer cave compositions were made under identical geomorphologic conditions. The residual soil products of many ages making up the cave deposits were all swept together into the cave opening in the same colluvial wash. Erosion would have occurred because of an ineffective vegetation mat indicating an overall drier climate. Butzer concludes that the same reasoning applies to the red, sandy cave-fill at Taung. This does not mean that the rates and modes of soil formation outside the caves did not vary through time, rather the suggestion was that variations in soil formation outside the caves were not contemporary with the periods of active erosion and consequent cave fillings. In general, the most recent evidence suggests that, at least in the Transvaal, all of the fossil hominids inhabited areas whose ecologies were not very different from the modern South African ones: a mixture of grassland and woodland that is never very arid or very wet.

The cumulative thickness of the cave deposits suggested to Butzer that the Transvaal cave-fills [illegible] a minimum of several tens of thousands of years and possibly several hundred thousands of years, which raises the question of contemporaneity of similar cave stratigraphy at two or more sites. In a recent review of the age of the South African cave fillings Partridge (1973) was able to place the different cave openings and fillings within a sequence of local erosional cycles and nickpoint recessions which resulted in a valley widening in areas where the cave sites were located.

He considered the following three drainage basins: (1) the Limpopo-Magalakwin-Makapan drainage system containing the Makapansgat limeworks site, (2) the Limpopo-Crocodile-Bloubank drainage system containing the Sterkfontein and Swartkrans sites, and (3) the Orange-Vaal-Harts-Buxton drainage system containing the Taung site at the Buxton lime quarry. Erosion within these drainage systems resulted in the retreat of the land surface and consequent exposure of cavern interiors to the outside. Once opened, the cavern was filled with externally derived hillside soil as well as with hominds and other animals.

Dating the earliest accumulation of the cave deposits requres that a determination be made of the time period which elapsed between the beginning of each new erosion cycle opposite the site locality and the recession of the valley side to the point of exposure of the cavern interior. From such an analysis a date of 3.7 million years was given for Makapansgat limeworks, 3.3 million years for Sterkfontein, 2.6 million years for Swartkrans and less than .9 million years for Taung, the deposit which accumulated on the valley flank at Buxton subsequent to the last erosion cycle. This work was criticized by Butzer (1974: 416).

As late as 1965 (Tobias 1965), the available faunal evidence from the Sterkfontein Type Site and Taung suggested a roughly contemporaneous age both sites belonging to the Sterkfontein Faunal Stage defined by Wells (1962) as consisting of species only 30% or fewer which could be identified with the present-day fauna.

However, on geomorphological grounds, Butzer (1974) has suggested that the Taung site may be more recent and lie closer to .7 m.y. than to 1.8 m.y. and Tobias (1974) has speculated that if this is correct then the Taung child may not be a member of the gracile australopithecine lineage at all but a member of the robust lineage as represented at Swartkrans.

Recent faunal analysis has also supported the contention that the Taung site is much younger than previously believed. Reviews of the primate fossils at Taung reveal that two species of *Papio* are found in common with those from Swartkrans and Kromdraai whereas the most common cercopithecoid, *Parapapio broomi*, from Sterkfontein and Makapansgat is absent from the Taung deposits. However the Taung fauna contains few bovids and relatively few taxa found at other sites, and most of this fauna comes from below the level of the australopithecine skull.

With a comparison of fossil suids from Sterkfontein and Makapansgat and that of *Elephas recki* from Makapansgat with those of the well-calibrated lineages from East Africa, Cooke (1970) suggested that the South African sites may be on the order of 2.5 - 3.0 million years old. Maglio (1973) agreed that these South African sites seemed to correlate best with the East African faunal succession equivalent to middle Shungura at Omo. Cooke has further suggested that Swartkrans is at least as old as Bed I, Olduvai (approximately 1.8 million years).

The most recent faunal analysis of the fossil remains at Sterkfontein has been completed for the Bovidae. The analysis of the fossil bovids provides interesting information concerning possible time differences between the two main hominid sites, STS and SE. Tobias has long believed that the hominid remains uncovered at the extension site (SE) were more advanced than the *Australopithecus* remains found at the type locality (STS) and the faunal comparison indicates that at least three distinct chrono-assemblages are present. As described by Vrba (1974), Phase A is associated with the STS australopithecine assemblage and is similar to that found at Makapansgat (Sterkfontein Faunal Span). Phase B is associated with the extension site

(SE) hominids and resembles both Kromdraai A and Swartkrans, though possibly closer to the latter in terms of species present and equivalent, therefore, to the Swartkrans or Cornelia Faunal Span. The similarity of tools from the SE site and from Swartkrans to the developed Olduwan assemblages has been reported by Mary Leakey (1970). Phase C is of Middle Stone Age (= Florisbad-Vlakkraal Faunal Span) and only two bovid species of the assemblage are extinct forms. (Locality D-16)

The evolution of bovids at Sterkfontein indicates a change in environmental conditions possibly because of a decrease in rainfall between Phases A and B (contra Brain 1958) which throws the problem of environmental reconstruction into further confusion. However, Vrba's (1974, 75) work shows that antilopine and alcelaphine antelopes are well represented throughout Sterkfontein-Swartkrans and Kromdraai. Such representation indicates a general persistence of relatively open vegetational settings and does not indicate any definite correlation of either type of australopithecine to a particular kind of vegetational setting.

The first published suggestion that some major South African fossil assemblages could be arranged in some chronological sequence (= Faunal Spans) was made by Wells (1962). Robinson's (1962: 98) attempt at correlation equated the "Middle breccia" at Sterkfontein with Swartkrans due to the presence of *Equus* at both sites. The age of the Makapansgat deposit was between that of Sterkfontein and that of Swartkrans (Ewer 1957). Climatic determinations by Brain indicated that the Middle breccia was a little later than the Limeworks Deposit and that the Sterkfontein Upper breccia appeared to be the same age as that of Swartkrans. Recent work by Vrba (1975) has suggested that the Swartkrans assemblage encompasses more than one component, one of which (SKB) is probably considerably later than the assemblage associated with the australopithecines (SKA). The present data also suggest that localities at Kromdraai, the faunal site (KA) and the australopithecine site (KB) as well as the Sterkfontein extension site (SE) should not be included in the Swartkrans Faunal span but rather perhaps in the succeeding Cornelia Faunal Span.

The patterns of accumulation of bone materials at the different sites have resulted in interesting speculations. According to Vrba (1975), Brain (1970), and Ewer (1967), the accumulation at the STS site is more likely to be the result of the action of large carnivores, possibly sabre-toothed cats. This would account for the high average weight determined for the bovid species represented in the assemblage. Brain (1970) has produced an interesting analysis that the predominant contribution to the SKA and KA assemblages may have come from leopards. The restricted medium weight range of the prey suggests smaller sized predators. In this light, the hominids from these localities are more likely to have been the prey than the predators.

The KB and SKB assemblages are different in that the bone remains are extremely fragmented and represent a high percentage of juvenile individuals, suggestive of a predator who specialized in small prey. With the evidence of the existence of stone tools at these sites (including locality D-16 at Sterkfontein with a Middle Stone Age industry), the suggestion was made (Vrba 1975: 303) that the predator in this case was a hunting hominid. Klein's (1977) analysis of the bone accumulation at Swartkrans and Kromdraai rests on the number of carnivore individuals found in any given stratigraphic unit within a site, and the fact that the carnivores varied respectively from 22% to [illegible] assemblage contains only 12% carnivores, but has some [illegible] each of the hominids as well as other cercopithecoids. This apparent specialization in terrestrial primate prey, in reality, masks the fact that a very large number of prey were also carnivores. The later SKB unit has revealed only 8.5% carnivores and fewer (3%) primates. This coupled with the fragmentary nature of the SKB assemblage again points to different agents of accumulation. Klein's interpretation, however, differs from that of Vrba because Kromdraai B contains some 17% cranivores and 50% primates out of a total 86 individual animals recovered and in this respect it is much more like SKA rather than the more recent SKB assemblage regardless of the fragmentary condition of the bones or of their age.

The large number of australopithecine fossils within the deposits may also reflect relatively high population densities. Klein (1977: 118) considers it unlikely that a carnivore would prey so heavily on very rare animals. The low proportion of adult individuals also indicates some degree of prey=size selection by the Kromdraai predators.

Finally at the Sterkfontein Extension Site (SE) the existence of numerous stone tools suggests that this locality may also have been a hominid occupational site. The accumulation pattern is different, however, from SKB and KB in that the assemblage is represented by species of all weight classes and that juveniles represent a markedly lower percentage in the remains. This data is consistent with the hypothesis that the SE remains are the result of hominid scavenger activity.

The pattern, therefore, of the bovid assemblages gives further evidence for establishing a relative sequence of events for some of the South African deposits: STS, SKA, KA, SE, KB, SKB and D-16 (older to younger).

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Includes plan of Sterkfontein excavation site (after Tobias and Hughes), distribution of bovid species between STS and SE, and suggested distribution of bovid species throughout all site units at Sterkfontein.

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Bovid fossil remains suggest a tentative chronology for the seven cave assemblages, from Sterkfontein, Swartkrans and Kromdraai, from which they are derived. They also suggest that, during the almost 2 million years of South African hominid and faunal Pleistocene history encompassed by this succession.

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CATALOGUE OF FOSSIL HOMINIDS
SWARTKRANS

Specimen #	Description	Found	Published
SK 1	Left M_2	1949	Trans. Mus. Mem. 9: 107
SK 2	Right I^1	1948	Trans. Mus. Mem. 9: 23
SK 3	Right I^2	1948	Trans. Mus. Mem. 9: 26
SK 4	Right $\underline{C}$	1948	Trans. Mus. Mem. 9: 41
SK 5	Left M_2	1949	unpublished
SK 6	Adolescent mandible, left P3$\rightarrow$M3, right P4$\rightarrow$M3, holotype *Paranthropus crassidens* Broom 1949	1948	Trans. Mus. Mem. 6
SK 7	Right P_4	1949	Trans. Mus. Mem. 9: 73
SK 8			
SK 9	Left P_4	1949	Trans. Mus. Mem. 9: 73
SK 10	Left corpus of mandible, M2-M3	1949	
SK 11	Maxillae with left P3-M3, right P3-M2	1949	Trans. Mus. Mem. 9: 60, 86, 91
SK 12	Mandible with left/right P4-M3, palate, mexilla	1949	Trans. Mus. Mem. 9: 60, 73, 112
SK 13/14	Maxillae, left P3-M3, right P3-M3	1949	Trans. Mus. Mem. 9: 55, 60, 81, 86, 90
SK 15	Mandible, left M1-3, right M2, M3 holotype *Telanthropus capensis*	1949	AJPA 11: 462
SK 16	Left M^3	1949	Trans. Mus. Mem. 9: 91
SK 17	Right M^1	1949	Trans. Mus. Mem. 9: 81
SK 18	Lower left P3, associated proximal end of radius	1949	AJPA 11: 462
SK 19	Right $\bar{M}$	1949	unpublished
SK 20	Left M_1	1949	unpublished
SK 21	Maxilla fragmented left C-M3	1949	unpublished
SK 22	Right M^3	1949	Trans. Mus. Mem. 9: 112
SK 23	Female mandible with teeth	1950	Trans. Mus. Mem. 9: 35, 36, 46, 69, 73, 101, 107, 112

SK 24	Left P^3	1949	Trans. Mus. Mem. 9: 55
SK 25	Mandible with left P4-M2, right P4-M2	1949	Trans. Mus. Mem. 6: 22
SK 26			
SK 27	Juvenile male (?) cranium, facial bones damaged, left I2, dm2, M1, right M1, unerupted C	1949	Trans. Mus. Mem. 6: 26-28
SK 28	Left P^3	1949	Trans. Mus. Mem. 9: 60
SK 29	Right $\overline{C}$	1949	Trans. Mus. Mem. 9: 46-48
SK 30	Left P_3	1949	Trans. Mus. Mem. 9: 69
SK 31	Right M^3	1949	Trans. Mus. Mem. 9: 91
SK 32			
SK 33			
SK 34	Mandible in two halves, left P4-M3, right I1-M3	1949	Trans. Mus. Mem. 6: 16-18
SK 35	Left M^1	1949	unpublished
SK 36	Right M^3	1949	Trans. Mus. Mem. 9: 91
SK 37	Mandible, left M2, M1	1949	Trans. Mus. Mem. 9: 107
SK 38	Right $\underline{C}$	1949	Trans. Mus. Mem. 9: 41
SK 39	Right P^4	1949	unpublished
SK 40	Left I^1	1949	Trans. Mus. Mem. 9: 23
SK 41	Right M^3	1949	Trans. Mus. Mem. 9: 91
SK 42	M^2	1949	unpublished
SK 43	Right P_4	1949	AJPA 11: 462
SK 44	P^3	1949	unpublished
SK 45	Right corpus mandible, M1-2	1949	Trans. Mus. Mem. 6: 111-112
SK 50	Male(?) right innominate, associated distal humerus	1949	Trans. Mus. Mem. 6: 90-94
SK 55/55b	Juvenile maxilla, left I^1-P3, M1, dm2, M2	1949	Trans. Mus. Mem. 9: 23, 26, 41, 55, 81, 69, 101, 112, 140

SK 57	Fragmented palate, left P3-M3, right P3-M1	1949	Trans. Mus. Mem. 9: 55, 60
SK 60			
SK 61	Juvenile mandible, right and left dI^1-dm2, erupting M1	1949	Trans. Mus. Mem. 9: 101, 130, 131, 134, 140
SK 62	Juvenile mandible, left dI2-dm2, M1 unerupted, right I^1-dm2	1949	Trans. Mus. Mem. 9: 35, 130, 131, 134, 140
SK 63	Juvenile mandible, left/right dc-dm2, m1	1949	Trans. Mus. Mem. 9: 35, 37, 46, 101, 131, 134, 140
SK 64	Juvenile mandible, right dm1, dm2	1949	Trans. Mus. Mem. 9: 134, 140
SK 65	Maxilla, left I^1-P4, right C	1949	Trans. Mus. Mem. 9: 23, 26, 41, 55, 60
SK 66	Juvenile maxilla, roots dc, dm1, dm2	1949	Trans. Mus. Mem. 9: 26
SK 67	Right I^1 possibly belonging to SK 65	1949	unpublished
SK 68	Left I^1	1949	Trans. Mus. Mem. 9: 23
SK 69	Left I^1	1949	Trans. Mus. Mem. 9: 23
SK 70	Left I^2	1949	Trans. Mus. Mem. 9: 26
SK 71	Right I^2	1949	Trans. Mus. Mem. 9: 26
SK 72	Left P_3	1949	Trans. Mus. Mem. 9: 69
SK 73	Right I^1	1949	Trans. Mus. Mem. 9: 23
SK 74a	Mandible with left P3-M2, right I2-M2	1949	AJPA 8: 299-300
SK 74b	Right I_1	1949	Trans. Mus. Mem. 9: 35
SK 74c	Right P^3	1949	unpublished
SK 75	Right M_3	1949	unpublished
SK 80	Fragmented maxilla, left I2-P3, same as SK 45	1949	Trans. Mus. Mem. 6: 111-112
SK 81	Left P_4, M_3	1949	Trans. Mus. Mem. 9: 73, 112
SK 82	Proximal right femur	1949	Trans. Mus. Mem. 6: 90-94

SK 83			
SK 84	First metacarpal	1949	Fossil Mammals of Africa 17
SK 85	Right $\underline{C}$/ fourth metacarpal	1949	tooth unpublished/Fossil Mammals of Africa 17
SK 86			
SK 87	Right $\overline{C}$	1949	Trans. Mus. Mem. 9: 46
SK 88	Left P_4	1949	Trans. Mus. Mem. 9: 73
SK 89	Left M^1	1949	Trans. Mus. Mem. 9: 81
SK 90	dm2, same as SK 89	1949	Trans. Mus. Mem. 9: 123
SK 91	dm1, same as SK 89	1949	Trans. Mus. Mem. 9: 128
SK 92	Right $\underline{C}$	1949	Trans. Mus. Mem. 9: 41
SK 93	Left $\underline{C}$, same as SK 85	1949	Trans. Mus. Mem. 9: 41
SK 94	Right lower (?) canine	1949	Trans. Mus. Mem. 9: 46,48 Wolpoff (1975): 251
SK 95	Left $\underline{C}$	1949	Trans. Mus. Mem. 9: 41,51
SK 96	Mandible, left, unerupted canine, P3	1949	Trans. Mus. Mem. 9: 46,69
SK 97	Proximal right femur	1949	Trans. Mus. Mem. 6: 90-94
SK 98	Left M^2	1949	Trans. Mus. Mem. 9: 86
SK 99	Left P^4	1949	Trans. Mus. Mem. 9: 60
SK 100	Right P_3	1949	Trans. Mus. Mem. 9: 69
SK 101	Left P^3	1949	unpublished
SK 102	Left M^1	1949	Trans. Mus. Mem. 9: 102
SK 103			
SK 104	Right M_1	1949	Trans. Mus. Mem. 9: 101
SK 105	Left M^3	1949	unpublished
SK 106			
SK 107			

SK 108			
SK 109			
SK 820	$\overline{C}$ unerupted	1952	Trans. Mus. Mem. 9: 46
SK 821	Portion of face with left P^3	1952	Trans. Mus. Mem. 9: 55
SK 822	Left P^3	1952	Trans. Mus. Mem. 9: 55
SK 823	Right P^3	1952	Trans. Mus. Mem. 9: 55
SK 824	Left P^4	1952	Trans. Mus. Mem. 9: 60
SK 825	Left P^4	1952	Trans. Mus. Mem. 9: 60
SK 826			
SK 826a	Maxilla fragment P3-M2	1952	Trans. Mus. Mem. 9: 86
SK 826b	Left P_4	1952	Trans. Mus. Mem. 9: 73
SK 827	Left P_4	1952	unpublished
SK 828	Left M_1	1952	Trans. Mus. Mem. 9: 101
SK 829	Left M^1	1952	Trans. Mus. Mem. 9: 81
SK 830	Left P_4	1952	Trans. Mus. Mem. 9: 73
SK 831	Right P_3	1952	Trans. Mus. Mem. 9: 69
SK 831a	Maxilla fragment, left M2-3	1952	Trans. Mus. Mem. 9: 86, 91
SK 832	Left M^1	1952	Trans. Mus. Mem. 9: 81
SK 833	Left M^1	1952	unpublished
SK 834	Left M^2	1952	Trans. Mus. Mem. 9: 86
SK 835	Left M^3	1952	Trans. Mus. Mem. 9: 91
SK 836	Left M^3	1952	Trans. Mus. Mem. 9: 91
SK 837	Right M^2	1952	Trans. Mus. Mem. 9: 86
SK 838			
SK 838a	Juvenile maxilla fragment, right dm2, m1,	1952	Trans. Mus. Mem. 9: 81, 128
SK 838b	left M_1	1952	Trans. Mus. Mem. 9: 101
SK 839	Juvenile maxilla fragment, left/ right di, dm2, m1	1952	Trans. Mus. Mem. 9: 81, 122, 128

SK 840	Left M_3	1952	Trans. Mus. Mem. 9: 112
SK 841a	Juvenile fragmented mandible, left dm2, ml	1952	Trans. Mus. Mem. 9: 140
SK 841b	Right M_3	1952	Trans. Mus. Mem. 9: 112
SK 842	Left dm_2	1952	Trans. Mus. Mem. 9: 140
SK 843	Adolescent left corpus mandible M1-M3	1952	Trans. Mus. Mem. 9: 101, 107
SK 844	Corpus mandible M2-M3	1952	Trans. Mus. Mem. 9: 112
SK 845	Crushed snout, left I2-M2, right I^1, P3-M1	1952	Trans. Mus. Mem. 9: 55, 60, 107
SK 846			
SK 847			
SK 848			
SK 849	Right M^1	1949	unpublished
SK 850	Right P_3	1949	unpublished
SK 851	Right M_3	1952	unpublished
SK 852	Juvenile mandible, left dm1-2, right dm1-2, M1	1952	
SK 853	Lumbar vertebra	1952	Robinson 1972: 101, 113-116
SK 854	Axis	1952	Robinson 1972: 101, 113-116
SK 855	Right M_3	1952	unpublished
SK 856	Right P^4, M^1	1952	unpublished
SK 857	Right P_3	1952	Trans. Mus. Mem. 9: 69-71
SK 858	Mandible, left I^1-M2, right I^1-M3	1952	Trans. Mus. Mem. 9: 35, 36, 101, 107
SK 859			
SK 860	Distal end of humerus	1952	unpublished
SK 861	Mandible fragment, left M1-2	1952	unpublished
SK 862	Mandible fragment, right M1 roots, M2-3	1952	unpublished
SK 863	Fragment $\underline{M}$ crown	1952	unpublished
SK 864	M_1(?) fragment	1952	unpublished

SK 865	Worn, crushed teeth	1952	unpublished
SK 866	Teeth fragments in breccia	1952	unpublished
SK 867	P^3 fragment	1952	unpublished
SK 868	Right M^2, M^3	1952	unpublished
SK 869	Juvenile mandible, fragment roots dml	1952	unpublished
SK 870	Left M^3 fragment	1952	unpublished
SK 871	Left M_3	1952	unpublished
SK 872	Left M^1	1952	unpublished
SK 873	Incisor fragment	1952	unpublished
SK 874	Crown fragment	1952	unpublished
SK 875	Crown fragment	1952	unpublished
SK 876	Mandible fragment, left C root, P3-M3, right I2-M3	1952	unpublished
SK 877			
SK 878	Two teeth and fragment calotte	1952	unpublished
SK 879	Four teeth fragments and associated bone fragments	1952	unpublished
SK 880	Right M_3 and 2 broken teeth	1952	unpublished
SK 881			
SK 882			
SK 883	Right M_3 and associated angle of mandible	1952	unpublished
SK 884	Right $\overline{C}$ and associated mastoid region	1952	unpublished
SK 885	Left M_3 associated with several broken teeth	1952	unpublished
SK 1512	Palatal fragment and teeth	1969	Nature 225: 1114
SK 1514	Mandibular fragment with roots	1969	Nature 225: 1114
SK 1524	Left M^2	1969	Nature 225: 1114
SK 1585	Cranial endocast of subadult	1966	Nature 225: 1114

SK 1586	Robust mandible, right I^{1-2}, M1-3, left I^1, M1-2	1965	Nature 225: 1114
SK 1587a	Left corpus mandible fragment P4, M1	1966	Nature 225: 1114
SK 1587b	Isolated right M_2 belonging to SK 1587a	1966	Nature 225: 1114
SK 1588	Left corpus mandible P4-M1	1966	Nature 225: 1114
SK 1589	Right P^4	1966	Nature 225: 1114
SK 1590	Two palatal fragments, right worn I2-M1, head of femur, and parts of an innominate	1965	Nature 225: 1114
SK 1591	Left M^1	1969	Nature 225: 1114
SK 1592	Palatal fragment with roots of molars	1969	Nature 225: 1114
SK 1593	Right P_3 worn	1966	Nature 225: 1114
SK 1594	Right M_1	1966	Nature 225: 1114
SK 1595	Fragment maxilla, left dm2	1969	Nature 225: 1114
SK 1596	$\underline{C}$ worn	1969	Nature 225: 1114
SK 1648	Anterior part of mandible, right M1-2 worn, left M1	1966	Nature 225: 1114
SK 3155b	Adolescent nearly complete ilium except for anterior superior iliac spine with acetabular portions of ischium and pubis		Day (1973): 33-34
SK 3974	Right M_1 crown	1967	Nature 225: 1114
SK 3975	Left M^3	1967	Nature 225: 1114
SK 3976	Left M_2	1967	Nature 225: 1114
SK 3977	Right M^3	1967	Nature 225: 1114
SK 3978	Infant mandible lacking rami, left dm1-2, right dm1-2, unerupted left M1	1967	Nature 225: 1114
SK 3981a	Last thoraic vertebra	1968	Nature 225: 1114
SK 3981b	Last lumbar vertebra	1968	Nature 225: 1114

SK 14000	*M*	1967	Nature 225: 1114
SK 14001	Left P^3	1967	Nature 225: 1114
SK 14003	Part of crushed skull, left M^1, right M1-3	1969	Nature 225: 1114

STERKFONTEIN

STS 1	Adult palate, left $P^3 \rightarrow M^2$, right $P^3 \rightarrow M^1$	1947	Trans. Mus. Mem. 9
STS 2	Juvenile snout with dm1-dm2, fragmentary maxilla with right dm1-dm2	1947	Trans. Mus. Mem. 4
STS 3	Right upper (?) canine	1947	Trans. Mus. Mem. 9: 44 Wolpoff (1975): 249
STS 4	M_2	1947	unpublished
STS 5	"Mrs. Ples" adult female, virtually complete cranium without teeth	1947	Nature 159: 672
STS 6	M_1 and M_2 probably belonging to STS 5	1947	Trans. Mus. Mem. 9: 110
STS 7	Old male mandible with dentition, scapula, proximal humerus	1947	Nature 160: 430
STS 8	Fragmentary maxilla $M^1 \rightarrow M^3$	1947	Trans. Mus. Mem. 9: 48
STS 9	Right M_1	1947	Trans. Mus. Mem. 9: 104
STS 10	Fragmentary maxilla M^2-M^3	1947	unpublished
STS 11	Left M^1, M^2	1947	unpublished
STS 12	Fragmentary maxilla, left $P^3 \rightarrow M^3$, right $P^4 \rightarrow M^2$	1947	Trans. Mus. Mem. 9: 57
STS 13	Snout with right dentition and part of left dentition, elderly adult	1947	unpublished
STS 14	Adult female, 9 thoracic, lumbar, sacrum, l/r innominates, proximal femur	1947	Trans. Mus. Mem. 4: 58-63
STS 16	$\underline{M}$	1947	unpublished
STS 17	Adult female fragmentary cranium with parietal, palate, left P3 → M1 and right P4 → M3	1947	Trans. Mus. Mem. 4: 24-25
STS 18	Juvenile mandible, left dm1, m1, dm2, right m1 → m2	1947	Trans. Mus. Mem. 9: 104
STS 19	Cranial base of STS 58	1947	Trans. Mus. Mem. 4: 27-33

STS 20	Fragmentary calvaria and endocranial cast	1947	unpublished
STS 21	Right M^2		Trans. Mus. Mem. 9: 84
STS 22	Left M^1, M^2	1947	Trans. Mus. Mem. 9: 88
STS 23	Right M^2	1947	unpublished
STS 24	Juvenile male? mandible with deciduous dentition	1948	Trans. Mus. Mem. 4: 42-43
STS 25	Inc. braincase	1948	unpublished
STS 26	Adult female? fragmentary cranium, left maxilla with M^3	1948	unpublished
STS 27	Fragmentary maxilla, left $P^3 \rightarrow M^3$ right $P^4 \rightarrow M^2$	1948	unpublished
STS 28	Right M^2, M^3, left M_1	1948	Trans. Mus. Mem. 9
STS 29	Adult palate $M2 \rightarrow M3$	1948	unpublished
STS 30	P^4, M^2	1948	Trans. Mus. Mem. 9: 62
STS 31	M^3	1948	unpublished
STS 32	Fragmentary maxilla $M^2 \rightarrow M^3$	1948	Trans. Mus. Mem. 9: 88
STS 33	$\underline{P}$	1948	Trans. Mus. Mem. 9
STS 34	Right distal femur	1948	Ann. Trans. Mus. 21: 181-182
STS 35	Fragmentary maxilla, left $P^3 \rightarrow M^2$	1948	unpublished
STS 36	Adult male? mandible, worn dentition	1948	AJPA 7: 123-127
STS 37	Left M^2, M^3	1948	Trans. Mus. Mem. 9: 88, 93
STS 38	Fragmentary mandible with RM_3	1948	unpublished
STS 39	Left P^4, M^1	1948	unpublished
STS 40	Fragmentary $\overline{c}$	1948	unpublished
STS 41	Mandible with left M_3	1948	Trans. Mus. Mem. 9: 114
STS 42	Adult palate, Right $P^3 \rightarrow M^3$	1948	Trans. Mus. Mem. 9: 58, 62
STS 43	$\overline{M}$	1948	unpublished

STS 44	Left M^2, M^3	1948	unpublished
STS 45	Fragmentary $\underline{M}$	1948	unpublished
STS 46	M^3	1948	unpublished
STS 47	P^3	1949	Trans. Mus. Mem. 9: 58
STS 48	Left $\underline{C}$	1949	Trans. Mus. Mem. 9: 44-45
STS 49	Fragmentary P_3	1949	unpublished
STS 50	Unerupted left $\bar{c}$ from TM 1516		Trans. Mus. Mem. 2: 65
STS 51	Right P_3, left $\bar{c}$	1949	Trans. Mus. Mem. 9: 48, 71
STS 52	Adult female (?) snout with maxillae and upper dentition	1949	Trans. Mus. Mem. 9
STS 52b	Mandible with dentition lacking ramus	1949	Trans. Mus. Mem. 9
STS 53	Adult palate, post-canine dentition	1949	Trans. Mus. Mrm. 9: 88, 93
STS 54	Right M^3	1949	Trans. Mus. Mem. 9: 93
STS 55	P^3	1949	Trans. Mus. Mem. 9: 58
STS 55b	Left M_3	1949	Trans. Mus. Mem. 9: 114
STS 56	M^1, M^2, dm2	1949	Trans. Mus. Mem. 9: 84, 88
STS 57	Fragmentary maxillae, left MP^3-M^1	1949	Trans. Mus. Mem. 9: 84
STS 58	Adult calvaria of STS 19	1947	Trans. Mus. Mem. 4: 27-33
STS 59	Left M_3	1949	unpublished
STS 61	Fragmentary maxilla, $P^3 \rightarrow M$	1949	unpublished
STS 62	Fragmentary mandible with worn [illegible]	[illegible]	unpublished
STS 63	Elderly adult, fragmentary face with orbit and some teeth	1949	unpublished
STS 64	Old adult palate, some teeth	1949	unpublished
STS 65	Right innominate, fragmentary pubis, left proximal femur, fragmentary certebral centrim	1949	Trans. Mus. Mem. 4: 58-63 Day (1973): 33

STS 66	Maxilla and palate, fragmentary dentition	1949	unpublished
STS 67	Fragmentary calvaria, associated M^3	1949	unpublished
STS 68	Proximal radius	1949	unpublished
STS 69	Fragmentary maxilla with some teeth	1949	unpublished
STS 70	Juvenile maxilla, deciduous dentition	1949	unpublished
STS 71	Fragmentary left side of calvaria, adult "skull 7"	1947	Broom *et*. *al*. (1950): 26
STS 72	Right M^3	1947-49	unpublished

STERKFONTEIN

Middle Breccia
"Extension Site"

SE 255	Juvenile maxilla M^1, dm^2, dm^1	1957	South Africa Archeol. Bull. 17: 102.
SE 1502	Right M^2	1957	South Africa Archeol. Bull. 17: 102.
SE 1579	Left $M^{1/2}$	1957	South Africa Archeol. Bull. 20: 187.
SE 1937	Left upper (?) canine	1958	South Africa Archeol. Bull. 17: 102. Wolpoff (1975): 249
SE 2396	Fragment left P^3	1958	South Africa Archeol. Bull. 20: 187.
SE 2398	Post-canine teeth, vertebra	1958	unpublished

TRANSVAAL MUSEUM SPECIMENS FROM STERKFONTEIN AND KROMDRAAI

TM 1511	Holotype *Plesianthropus transvaalensis*; young adult male cranium with occipital, maxillae, right $P^4 \rightarrow M2$, left $P3 \rightarrow M2$	1936	Nature 138: 486
TM 1512	Maxilla, M3 adult female right maxilla $I2 \rightarrow M1$	1936	Ann. Trans. Mus. 19: 339-373
TM 1513	Distal left femur	1936	Trans. Mus. Mem. 2: 73-75
TM 1514	Old adult male? left maxilla, M^3	1936	Trans. Mus. Mem. 9: 49-50
TM 1515	Old adult male? mandible left $P_3 \rightarrow M_2$	1936-38	Trans. Mus. Mem. 2: 54
TM 1516	Juvenile symphysis, unerupted 1/RC	1936-38	Trans. Mus. Mem. 2: 53
TM 1517 (Kromdraai)	Left cranium, teeth and postcranial bones, holotype *Paranthropus robustus*	1938	Trans. Mus. Mem. 2: 84-118
TM 1518	Right M_3	1938	Ann. Trans. Mus. 19: 339-373
TM 1519	Worn right M_3	1938	Trans. Mus. Mem. 2: 67
TM 1520	Worn left M_3	1938	Trans. Mus. Mem. 2: 67
TM 1522	Ramus mandible	1936-38	unpublished
TM 1523	Left P_4	1938	Ann. Trans. Mus. 19: 339-373
TM 1524	Root M^1	1938	unpublished
TM 1526	Capitate	1936	Trans. Mus. Mem. 2: 73-75
TM 1527	Right $\underline{C}$	1938	Trans. Mus. Mem. 2: 57
TM 1528	Fragment right upper (?) canine	1938	Ann. Trans. Mus. 19: 339 Wolpoff (1975): 249
TM 1532	Left M^3	?	unpublished
TM 1534	Worn $\overset{=}{I}$	1938	unpublished
TM 1535	Upper canine of TM 1514	1938	Trans. Mus. Mem. 9: 56
TM 1536 (Kromdraai)	Juvenile female? mandible deciduous dentition	1941	Nature 147: 607

TM 1561	Right M^3	1938	Trans. Mus. Mem. 2: 57
TM 1600 (Kromdraai)	Mandible fragment, left P_3, M_2, M_3	1954	unpublished
TM 1601 (Kromdraai)	dm_1, $\vec{C}$, P_3, P_4, M^1	1954	unpublished
TM 1602 (Kromdraai)	Fragmentary right maxilla, M^1–M^3	1938?	unpublished
TM 1603 (Kromdraai)	Left M^3 from TM 1517	1944	Trans. Mus. Mem. 9: 92
TM 1604 (Kromdraai)	Left dm_2	1955	unpublished
TM 1605 (Kromdraai)	Ilium, part of acetabulum, lacking iliac crest	1954	unpublished
TM 3601	Distal femora with broken femoral condyles	?	Day (1973): 37-38

AUSTRALOPITHECINE REMAINS FROM MAKAPANSGAT LIMEWORKS

NUMBER	FRAGMENT	DATE DISCOVERY	DESCRIPTION
MLD 1	Calvaria	1947	AJPA (1948) 6: 259
MLD 2	Adolescent mandible	1948	AJPA (1948) 6: 301
MLD 3	Parietal fragment	1948	AJPA (1949) 7: 187
MLD 4	Left M3 isolated	1948	AJPA (1949) 7: 203
MLD 5	Right M2 isolated	1948	AJPA (1949) 7: 201
MLD 6	Cranio-facial fragment ("1st palate")	1948	AJPA (1949) 7: 187
MLD 7	Left ilium	1948	AJPA (1949) 7: 301
MLD 8	Right ischium	1948	AJPA (1949) 7: 301
MLD 9	Premaxillo-maxillary fragment ("2nd palate")	1948	AJPA (1949) 7: 335
MLD 10	Biparieto-occipital fragment	1948	Zeitschr. f. Morphol. u. Anthropol., 1955
MLD 11	Part of infant maxilla	1949	undescribed
MLD 12	Right M3 isolated	1949	undescribed
MLD 13	Isolated upper C hominid ?	1949	Wolpoff (1975): 251
MLD 14	Humeral right shaft fragment	1949	L'Anthropol., 1955
MLD 15	Distal right extr. radius	1949	L'Anthropol., 1955
MLD 16	Proximal right extr. radius	1949	L'Anthropol., 1955
MLD 17	Head of femur	1949	L'Anthropol., 1955
MLD 18	Adult mandible	1953	AJPA (1954) 12: 313
MLD 19	Left M3 and mandibular fragment	1955	AJPA (1962) 20: 269
MLD 20	Acrom. extr. right collar bone	1955	undescribed
MLC 1	Right M1 and 2 maxillary fragment	1955	Nature
MLD 21	Very fragmentary ilium	1955	unpublished

NUMBER	FRAGMENT	DATE DISCOVERY	DESCRIPTION
MLD 22	Left fragment mandible, $M_2 \rightarrow M_3$ and sockets of $M_1 \rightarrow P_3$	1953	AJPA (1962) 20(3): 269
MLD 23	Very fragmentary left maxilla with I^2, P^3 same as MLD 6	1955	unpublished
MLD 24	Left M_2	1956	AJPA (1962) 20(3): 269
MLD 25	Juvenile left ilium	1956	AJPA (1958) 16: 473
MLD 26	Fragmentary frontal	1956	undescribed
MLD 27	Symphyseal region of mandible, sockets of incisors and canines and roots of P_3	1956	AJPA (1962) 20(3): 269
MLD 28	Fragmentary right maxilla with palate M^2, M^3	1956	undescribed
MLD 29	Symphyseal region of mandible with fragment of left horizontal ramus	1956	AJPA (1962) 20(3): 269
MLD 30	Associated piece with MLD 11	1949	Trans. Mus. Mem. 9: 28, 45, 59, 63
MLD 31	Right temporal, mastoid, tympanic	1956	undescribed
MLD 32	Proximal extr. left radius	1956	undescribed
MLD 33	Fragmentary right parietal (?), possibly cercopithecoid	1956	undescribed
MLD 34	Right one-half of horizontal ramus of mandible with roots of $M_1 \rightarrow M_2$	1960	AJPA (1962) 20(3): 269
MLD 35	Frag. infant ilium (?)	?	undescribed
MLD 36	Left acromial extr. clavicle	1960	undescribed
MLD 37/38	"Makapansgat skull" adult female cranium, fragmentary maxillae with right $M^1 \rightarrow M^3$ and left M^2	1958-59	AJPA (1962) 20(2): 119
MLD 39	Right distal humerus	1958	Nature (1962) 191: 372
MLD 40	Fragmentary left mandible with $C \rightarrow M_2$	1961	AJPA (1962) 20(3): 269

FIGURE 11-8

Fossil Hominid Bearing Sites in East Africa

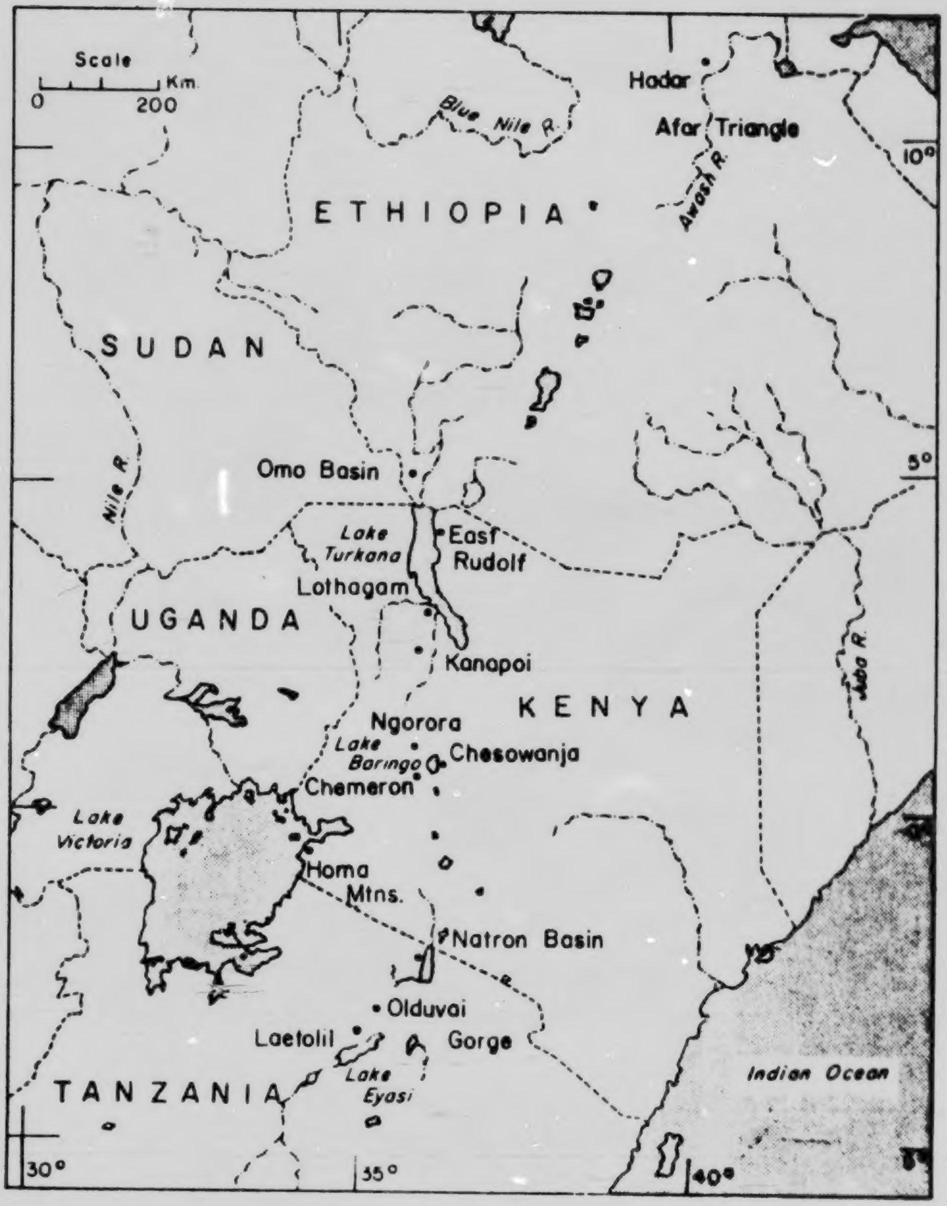
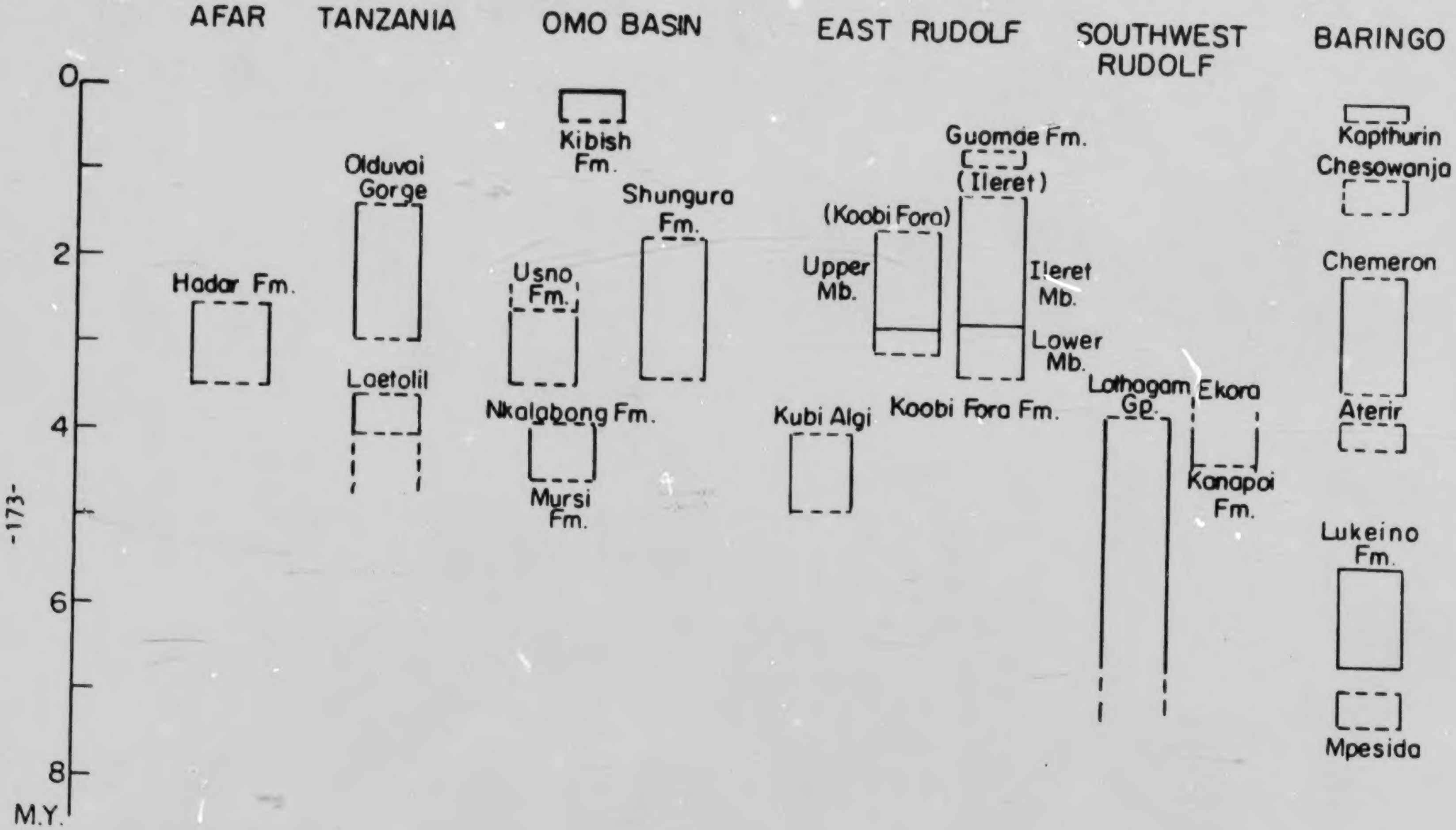

Scale
0
200
Km.
Blue Nile R.
Hadar
Afar Triangle
Awash R.
10°
ETHIOPIA
SUDAN
Nile R.
Omo Basin
5°
Lake Turkana
East Rudolf
Lothagam
UGANDA
Kanapoi
Juba R.
KENYA
Ngorora
Lake Baringo
Chesowanja
Chemeron
Lake Victoria
Homa Mtns.
Natron Basin
Olduvai Gorge
Laetolil
Lake Eyasi
TANZANIA
Indian Ocean
30°
35°
40°

FIGURE 11-9



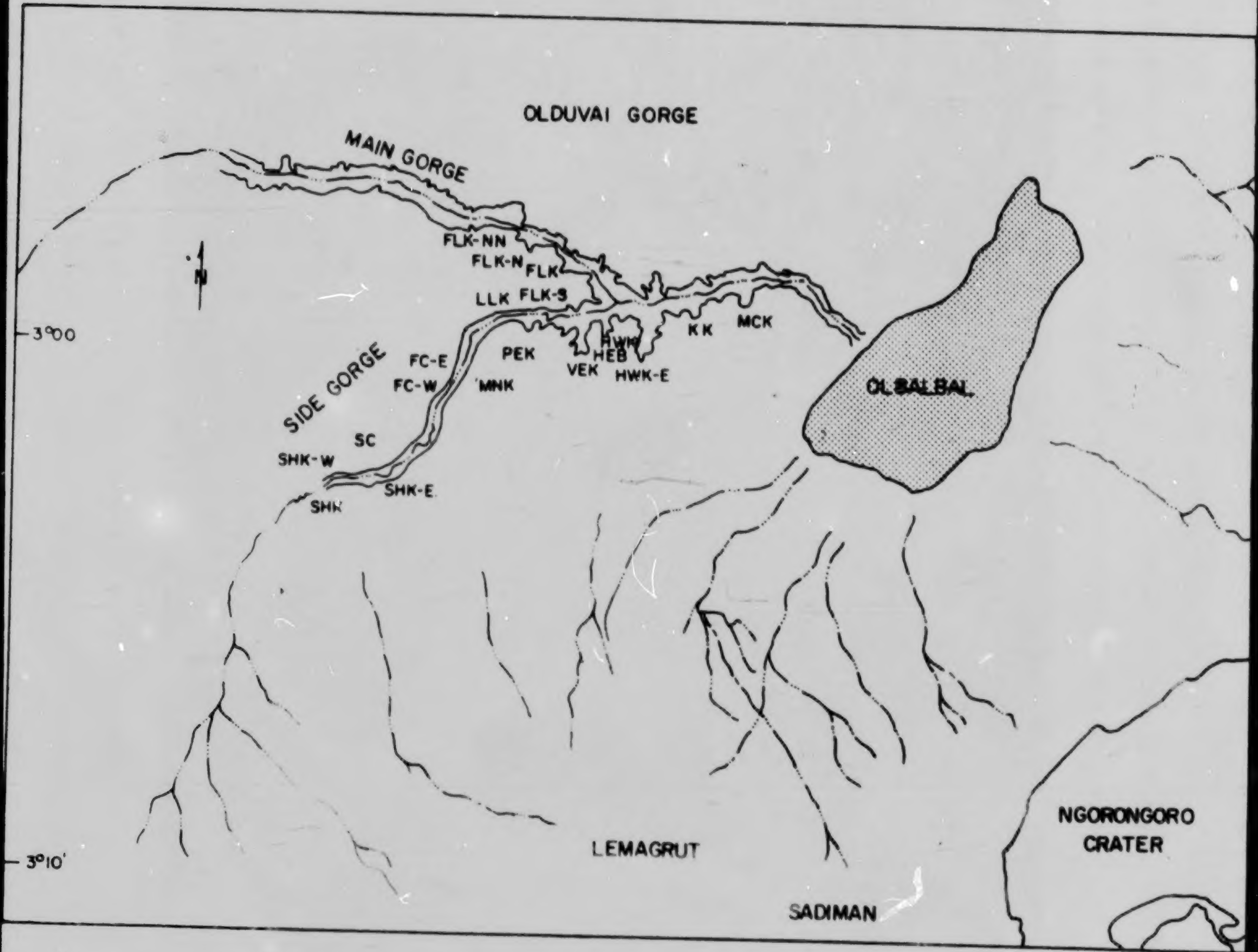
STRATIGRAPHIC CORRELATIONS. (Redrawn from Behrensmeyer, 1976)

AREA II

Tanzania

Olduvai Gorge
Laetolil

FIGURE II-10


OLDUVAI GORGE
MAIN GORGE
SIDE GORGE
FLK-NN
FLK-N
FLK
LLK
FLK-S
KK
MCK
HWK
HEB
PEK
VEK
HWK-E
FC-E
FC-W
MNK
SC
SHK-W
SHK-E
SHK
OLBALBAL
N
3°00
3°10'
LEMAGRUT
SADIMAN
NGORONGORO
CRATER

OLDUVAI GORGE. Main site localities

OLDUVAI GORGE

Geochronology

Cut in the Serengeti Plains Olduvai Gorge lies 46 km on roughly a west to east gradient emptying into a depression, Olbalbal, on the base of the western face of the Ngorongoro crater (Figure II-10). The main branch of the gorge is known as the Main Gorge having its origin in Lake Ndutu. The Main Gorge is broad and shallow and underlain by a basement complex of metamorphic rocks. About 9 km from the eastern end, the Main Gorge is joined by a smaller southern branch known as the Side Gorge which originates on the western slopes of Lemagrut volcano, a deeply eroded volcano to the west of Ngorongoro.

Separating the Olduvai sediments from metamorphic basement rocks is a single welded tuff, the Naabi Ignimbrite probably originating from eruptions of Ngorongoro. The term Olduvai Beds was originally applied to Beds I through V. Modern usage, now takes into account all of the sediments from Bed I through the Naisiusiu Bed, eolian tuffaceous deposits of recent origin. The youngest deposits are ash and alluvium of Holocene age. The various "Beds" can be considered formations which are subdividable into additional deposition units.

Olduvai Gorge was discovered in 1911 by Professor Kattwinkel who also collected a sample of fossil mammals. Following this initial work, a German expedition was led by Professor Hans Reck who recovered additional fossils and studied the geology of the lower Gorge. Reck published his work in 1914.

In 1931 L.S.B. Leakey led the first archeological expedition to Olduvai. Joined by Reck the lower Gorge was again investigated and the geological summary was published by Reck (1951) in the first of a series of volumes on Olduvai Gorge. Again in August, 1932, Leakey revisited the Gorge with E.J. Wayland, director of the Geological Survey of Uganda. Leakey and Wayland determined that the first fossil hominid (OH-1) the Olduway skeleton, earlier discovered by Reck, originated in Bed V rather than Bed II, a view favored by Reck.

At intervals from 1935 onward L.S.B. and Mary Leakey studied the archeology and paleontology of the Gorge. Leakeys interpretations of the stratigraphy in terms of pluvial and interpluvial periods has been criticized by Cooke (1957) and Flint (1959). The most recent geological investigations of G. Curtis and J. Everden began with the K-Ar dating which gave an age of 1.75 m.y. for Bed I. In 1961 the entire Gorge was mapped by R. Pickering, who also provided a detailed map of the FLK site. None of this work has been published. Following this work M. Kleindienst completed a series of archeological explorations of site JK II clarifying some of the geological deposits of Bed II and IV. In 1962 R. Hay began work in the stratigraphy of the Bed I tuffs (Hay 1963). Hay returned to Olduvai in 1964 to complete his investigations of the geology of the Gorge and concentrated his efforts on Beds II, III, and IV and on the extensive faulting which began at Olduvai during the deposition of Bed II. Laboratory analysis of samples collected at Olduvai showed that the Olduvai Beds were divisible into a series of mineralogic zones which were then correlated with various depositional environments, and also left no doubt that the lake in which Beds I and II were deposited was variably saline and alkaline in composition. Studies also showed that the lake fluctuated considerably in level and extent. Hay continued work at the Gorge from 1970 through 1974 and produced a detailed stratigraphy of Bed II. The culmination of the geological investigations is Hay's recently published monograph, Geology of the Olduvai Gorge (1976).

The exposed Olduvai sequence is as much as 100 m in thickness deposited in a saline lake of approximately 25 km in diameter. The Olduvai Beds are subdividable into seven lithostratigraphic units now labeled Bed I, Bed II, Bed III, Bed IV, the Masek Beds, the Ndutu Beds and the Naisiusiu Beds Chromostratigraphically these deposits span a period from about 2.1 m.y. to 15,000 yr. B.P.

Bed I is the thickest of the lithostratigraphic units, up to 60 meters in the eastern part of the Main Gorge. The previous designations of Lower members, Basalt mambers and Upper members (Hay 1971) have now been abandonded. Bed I is subdivded into five lithofacies which consist of lavas overlain by sediments of lake, lake margin and alluvial deposition, lying between the Naabi Ignimbrite and including the lava flows at the bottom of the Gorge to the base of Bed II (Hay 1976). Within the sedimentary sequence are several widespread tuffs which serve as marker beds. The oldest of the lithofacies are 2.0 - 2.1 m.y. and the uppermost have yielded an average age of 1.70 m.y.

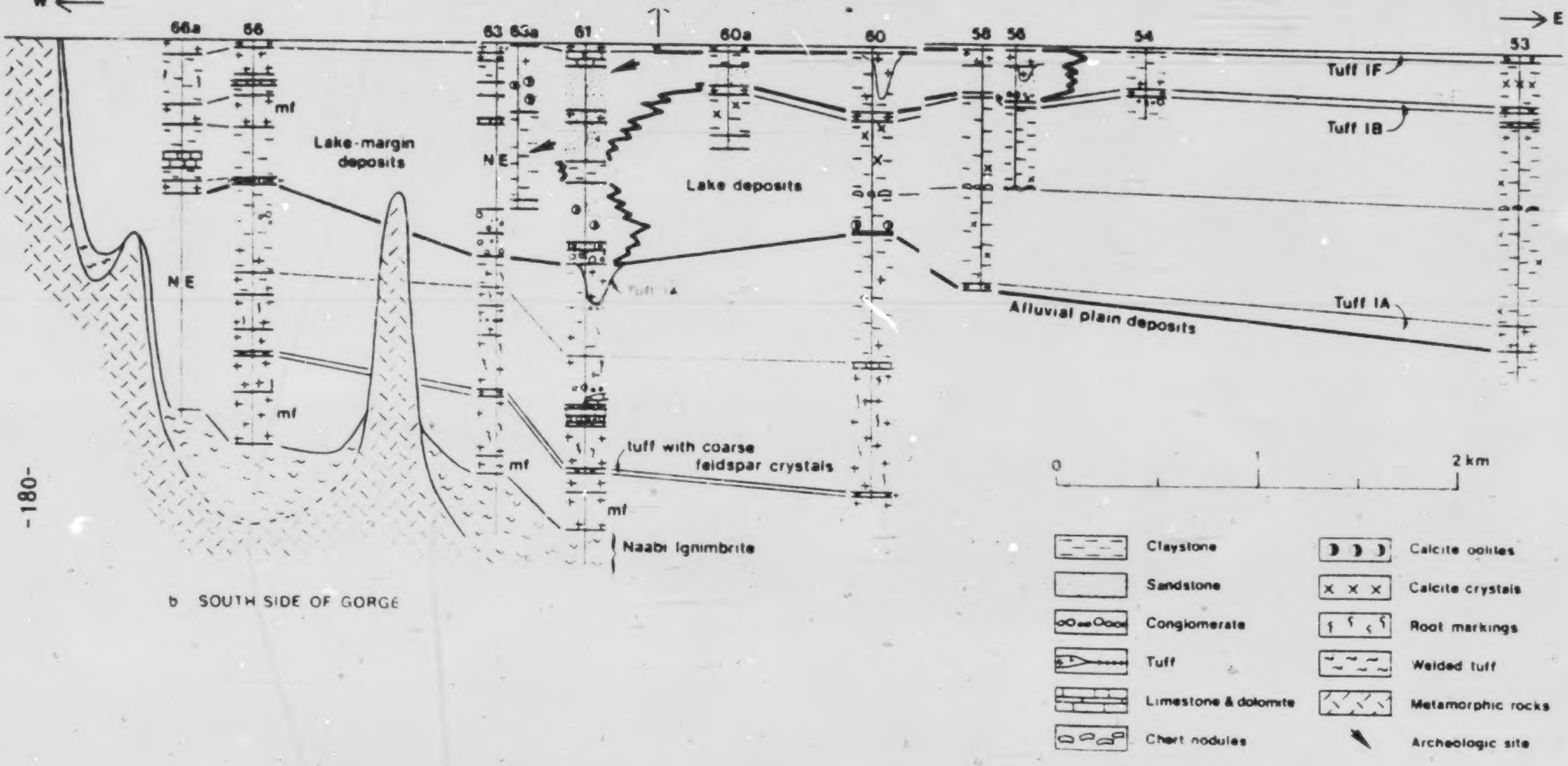
Lake-margin deposits resulted in the flooding of the lake by fresh water and deposits in this area contain the vast majority of the faunal and archeological remains. The lava flows form a thick sequence which underlie the sediments, the lowermost lavas originated in eruptions from Olmoti and the uppermost flows from vents to the south of the Gorge. Tuffs within the sediments originated from eruptions of Olmoti and Ngorongoro. Six tuffs provide the principal basis for correlation within Bed I, termed I^A - I^F (Hay 1971). All, except Tuff I^B and I^E which are ash-flow tuffs, are air-fall tuffs. The oldest of the artifacts and hominid remains have been recovered from below Tuff I^B which has been satisfactorily dated at 1.79 ± .03 m.y. In total fifty-seven K-Ar dates have been obtained from Bed I. Besides the

K-Ar dates a fission-track date of 2.03 ± 0.28 m.y. was obtained from glass fragments from Tuff I^B (Fleischer et al. 1965) which is significant in confirming the results from the K/Ar determinations.

Paleomagnetic studies of Bed I suggest that the base of the Olduvai Normal Event lies below Tuff I^A. This normal polarity overlies a series of reversed welded Tuffs in the lower part of Bed I dated to 2.0 - 2.- m.y. The upper limit of the Olduvai event appears to be on or near the base of the Lemuta Member of Bed II (Grommé and Hay 1963, 1967, 1971). Bed II is 20 to 30 m thick and is found over a slightly larger area than Bed I. Its stratigraphy is complex and following Reck's usage it is taken to include the deposits between Tuff I^F and the reddish-brown sediments of Bed III. Site JK may be considered a type section. Bed II conformably overlies the sediments of Bed I which differs from the sharp disconformable contact above with Bed III.

Bed II can be subdivided into many individual beds and tuffs which can be used for purposed of correlation. The Lemuta Member (formerly the Eolian Tuff Member (Hay 1967)) is a widespread, distinctive sequence of eolian tuffs with a maximum thichness of 14.5 m. The Lemuta Member underlies a regional disconformity dated to about 1.60 m.y. which subdivides Bed II into two major units differing in lithology and Paleogeographic setting. Deposits below the disconformity have many features in common with Bed I, whereas the overlying deposits are unique in many respects to the remaining Olduvai sequence. The lower disconformity marks the beginning of widespread faulting and folding, the increased area of grassland, a decreased size of the lake and an abrupt change in the fossil fauna. The deposits of Bed II span the period from about 1.70 to about 1.15 m.y.

FIGURE II- 11


W
E
66a
66
63
63a
61
60a
60
58
56
54
53
15 m
0
Tuff IF
Tuff IB
Tuff IA
Lake-margin deposits
Lake deposits
N E
mf
Alluvial plain deposits
tuff with coarse feldspar crystals
Naabi Ignimbrite
0
1
2 km
b SOUTH SIDE OF GORGE
Claystone
Sandstone
Conglomerate
Tuff
Limestone & dolomite
Chert nodules
Calcite oolites
Calcite crystals
Root markings
Welded tuff
Metamorphic rocks
Archeologic site

BED I, OLDUVAI GORGE. South Side of Main Gorge
Stratigraphic sections and lithofacies
(From Hay, 1976: 30-31)

Geologically the lower part of Bed II continues the lithofacies common to Bed I consisting of lake and lake-margin deposits, alluvial-fan deposits and eolian deposits. Above the lower disconformity are further lake deposits, fluvial-lacustrine deposits and fluvial deposits. Most of the known faunal remains of Bed II above the disconformity have been recovered from the fluvial sandstones and conglomerates concentrated in a main channelway that drained into the east end of the lake.

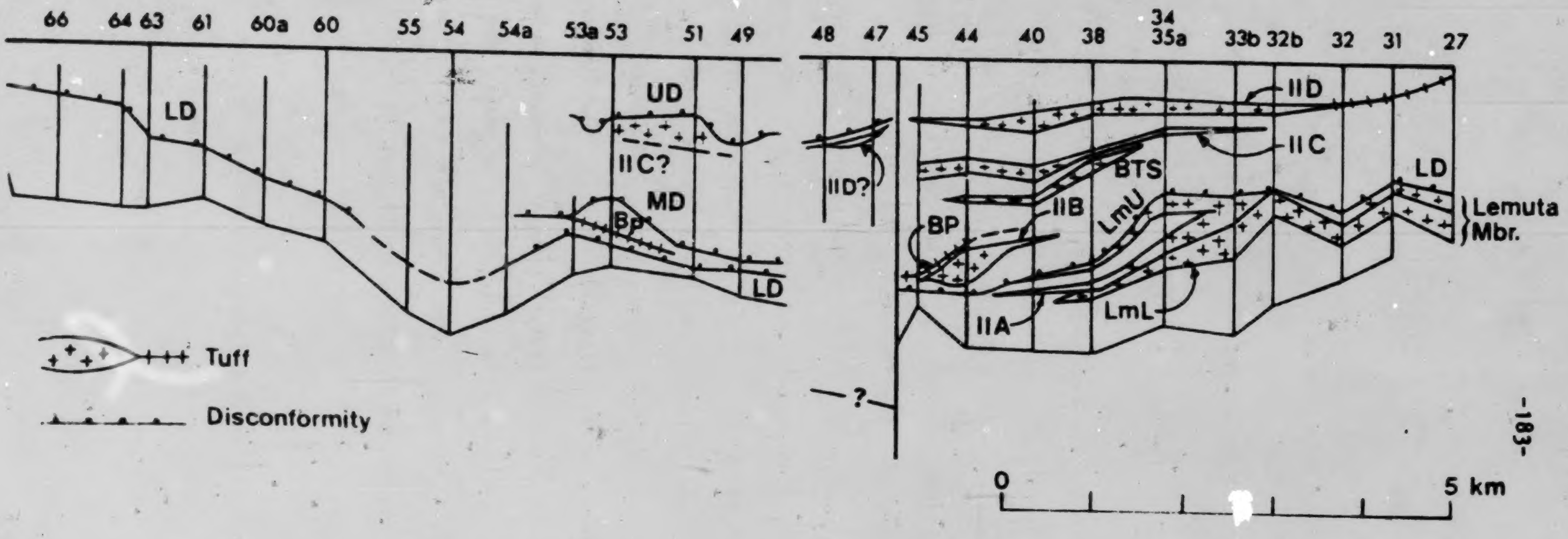
The four principal marker tuffs have been designated Tuffs II A-D (Hay 1971) and are typically reworked and discontinuous. In addition the "bird-print tuff" lying between tuffs II^B and II^C is significant in correlating the eastern and western parts of the Main Gorge.

Potassium-argon dating of Bed II has proved unsatisfactory primarily because of the reworking and thus contamination of the tuffs. The only reasonably consistent date comes from Tuff II^A yielding the youngest date on the least reworked sample of 1.71 m.y. (Curtis and Hay 1972). The best known Bed II date of 0.50 m.y., supposedly from site SHK, is unacceptable because all of the tuffs in this area are contaminated by grains from the metamorphic basement. One date from a level above Tuff II^D at SHK gave an age of 80.0 m.y. ! (Curtis and Hay 1972)

Paleomagnetic determinations point to an age of 1.70 m.y. for the base of Bed II. The top of the Olduvai Event of normal polarity extends to the base or within the lowermost units of the Lemuta Member. Polarity measurements by A. Brock and A. Cox show reversed rocks above the Lemuta Member to the base of Tuff IV^B in the middle of Bed IV representing the reversed portion of the Matuyama epoch. If the Brunhes - Matuyama boundary lies somewhat above the middle of Bed IV and is dated at 0.7 m.y. then, on the basis of the thickness of the sedimentary sequence from the top of the Lemuta Member to Tuff

IV^B, the top of Bed II should be about 1.15 m.y. This date is in agreement with that determined for the disconformity and fault displacement at Olduvai correlated to a major phase of Rift-Valley faulting occurring eastward dated by Macintyre _et al_. (1974) at 1.15 - 1.2 m.y.

FIGURE II-12


66
64
63
61
60a
60
55
54
54a
53a
53
51
49
48
47
45
44
40
38
34
35a
33b
32b
32
31
27
LD
UD
IIC?
MD
Bp
LD
IID?
BP
IIB
BTS
LmU
IID
IIC
LD
Lemuta Mbr.
IIA
LmL
?
Tuff
Disconformity
0
5 km

BED II, OLDUVAI GORGE, Main Gorge
Marker Tuffs and Disconformities

Tuffs	IIA-D
LmL/U	lower/upper unit of Lemuta Mbr.
BP	bird print tuff
BTS	brown tuffaceous siltstone
LD	lower disconformity
MD	middle disconformity
UD	upper disconformity

(From Hay 1976: 58-59)

Biostratigraphy

The faunal sequence at Olduvai has recently been the subject of many reports and is of immense importance to environmental interpretations. The most up to date faunal list for Bed I is presented on Page 294. Additional work includes that of J.J. Jaeger (in press) on rodents, and A. and A. Gentry on bovids (in press).

The Olduvai fauna can be subdivided into two major units at the disconformity occurring above the Lemuta Member of Bed II. The lower unit is a predominantly swamp-dwelling assemblage, whereas in the upper unit the proportion of savannah-dwelling animals abruptly increases. Within the lower unit between the "Zinjanthropus" level and Tuff I^{F}, there is also a significant difference in bovid types between the upper and lower horizons. The commonest bovid remains at sites DK and FLK NN are of Reduncini which present-day speices are found to live always close to water. At FLK N (the uppermost fossilferous levels in Bed I) the Reduncini are rare and the most common form are the Alcelaphini, which are more characteristic of drier open country (Hay 1976 : 47) The fossil avifauna indicate that, in general, however, water was much more plentiful throughout the time of the deposition of Beds I and II than is the case at present. Aquatic birds are more common below Tuff I^{C} and land birds are most common in levels at FLK-N confirming the hypothesis for a drier period during the deposition of uppermost levels of Bed I suggested by the bovid data.

The evidence of hominid activities in Bed I comes predominantly from the eastern lake-margin deposits. Fourteen hominid fossils have been recovered from sediments in this area and in addition, eighteen archeologic sites have been discovered. The hominid material occurs at many levels between the lavas and Tuff I^F. (Figure 11-13) in localities generally coinciding with the fluctuating edge of the Lake. Paleobotanical and Paleontological evidence from Site DK which yielded the stone circle and occupation site, Site FLK-NN and Site FLK (the "Zinjanthropus" floor) indicate marsh, or swamp or lake shore environments. Large quantities of crododile, numerous fish and amphibian remains, together with bones of waterfowl and abundant rootcasts of marshland vegetation testify to the prescence of nearby permanent water.

The regional disconformity subdividing Bed II marks an abrupt change in the fauna. The predominantly swamp-dwelling forms continuing from Bed are replaced by forms favoring open savannah and riverine conditions. However, the abrupt increase in proportion of the savannah forms reflects the paleographic change caused by faulting rather than a rapid change in climate (Hay 1976:111). The geologic evidence of greater salinity of the Bed II lake over that of Bed I, the deposition of coarse conglomerates and mudstones suggestive of flash floods caused by torrential downpour and the abundant limestones and dolomites point to a semiarid climate which prevailed throughout the period of deposition of Bed II.

Sixteen of the Olduvai Hominid fossils are derived brom Bed II sediments. (Figure II.) Remains assignable to Homo habilis (OH 13, 16, 37, 41) have been found only below the level of Tuff II^B. The remains of the more advanced Homo erectus (OH 9, 36) have only been recovered near the top of Bed II at or above the level of Tuff II^D. Remains of the robust australopithecine, A. cf boisei (OH 3, 20, 26, 30), occur throught the levels of Bed II. Sixty-three archeologic sites representing the sequence: Olduwan—— Developed Olduwan A and B Acheulian have also been discovered within the Bed II sequence.

The Olduwan characterized by choppers, polyhedrons, discoids, scrapers and other forms is found from the base of Bed II to near the level of Tuff II^B. The Developed Olduwan A, which is marked by an increase in spheroids and in the number and variety of light-duty tools, is found associated only with the lower augitic sandstone lying between the lower and middle disconformities. The lowest site of Developed Olduwan B lies immediately below the upper augitic sandstone extending into the uppermost sites above Tuff II^D. Developed Olduwan B is different from A in that bifaces are present, though in negligible proportion to the other tool types. Sites where bifaces characterize 40% or more of the tool types have been classified as Acheulian (Leakey 1971:1-2). Only one Acheulian site at EF-HR lying above the brown tuffaceous siltstone has been described. However, M. Leakey (1971) has classified an additional eight other sites as Acheulian. Two sites (Loc 32 and Loc 12a) may be stratigraphically equivalent to the upper part of the upper augitic sandstone. This represents the oldest known occurence of bifaces at Olduvai of the Acheulean type (1.4-1.5m.y.). Another site (CK, loc7) lies between Tuffs II^C and II^D and the remaining six sites are located stratigraphically above Tuff II^D. The concentration of archeologic sites in Bed II are found in the eastern fluvial-lacustrine deposits and may reflect a relatively stable supply of fresh water. Sites of the Acheulian type are found in 9 out of 10 cases 1 km or more from the lake shoreline, whereas seven of the Olduwan B are lake margin in location. The correlation between industry and paleogeography thus seems significant (Hay 1976:114).

FIGURE II-13

Hominid Sites, Stratigraphic Relationships
and Radiometric Dates, Olduvai Gorge

	Disconformity			
	Tuff IID	Homo	LLK II	OH 9, 36 38
	upper disconformity	erectus	BK II	OH 3
	Tuff IIC			
	brown tuffaceous siltstone			
	upper augitic sandstone		FC West	OH 19
	middle disconformity			
	bird-print tuff			
	Tuff IIB	Homo	MNK II (skull site)	OH 13-15, 32?
	lower augitic sandstone	habilis	SC II	OH 40, 41, 37?
	main chert unit		FLK West	OH 26
	lower disconformity			
BED II	Tuff IIA			
	Lemuta Member (=Eolian Tuff Mbr.)		HWK J. East	OH 27
			HWK II	OH 20
			FLK II Maiko Gully	OH 16, 30
	Tuff IF (=Marker Bed B) 1.7 m.y.		FLK NI	OH 10
	Tuff IE			
	Tuff ID ?1.71 m.y.		FLK I	OH 5, 6
			FLK NNI	OH 7, 8, 33
BED I	Tuff IB 1.79 ± .03 m.y.		DK I East	OH 24
			MK I	OH 4
	Lavas (=Basalt Mbr.) ?1.85 m.y.			
	Naabi Ignimbrite ?2.4 m.y.			

OLDUVAI GORGE

Fossil Inventory

Found	Number	Site	Description	Published
1913	OH 1	BK II	Burial - complete skeleton	Reck, 1914
1935	OH 2	MNK IV	Parietal fragments	Leakey, 1951: 160
1955	OH 3	BK II	Ldm^2	Leakey, 1958
1959	OH 4	MK I	*Homo habilis* fragment L. mand. (M$_3$)	Leakey, Tobias, Napier, 1964
1959	OH 5	FLK I	*Australopithecus boisei* cranium (Type) palate and upper dentition	Tobias *in* Leakey, 1967
1959	OH 6	FLK Main	*Homo habilis* isolated teeth (LM^1, $\underline{I}$, LP$\underline{3}$)	Leakey, Tobias, Napier, 1964
1960	OH 7	FLK NN I	*Homo habilis* mandible (Type) (LI, -M$_2$, RI, -M$_1$), L/R juv. parietals	Leakey, 1961b
1960	OH 8	FLK NN I	*Homo habilis* L Pes, 7 tarsals, 5 metatarsals	Day, Napier, 1964
1960	OH 9	LLK II	*Homo erectus* calvaria	Leakey, 1961
1961	OH 10	FLK N I	Terminal phalange	Day, Napier, 1966
1962	OH 11	DK IV	L maxilla, palate, teeth C-M$_2$	Tobias *et*. *al*., 1
1962	OH 12	VEK IV	Calotte, palate, teeth P$_3$-M$_2$	Leakey, Leakey, 1
1963	OH 13	MNK II	Calvaria, R maxilla, palate P$_3$-M$_3$ mandible, complete dentition distal humeral shaft?	Leakey, Tobias, Napier, 1964
1963	OH 14	MNK II	Juv. calotte parietal, L/R temporal frontal	Leakey, Tobias, Napier, 1964
1963	OH 15	MNK II	*Homo* sp. isolated teeth (LM^3, RM^3, RC)	Leakey, Tobias, Napier, 1964
1963	OH 16	FLK II Maiko Gully	*cf*. Australopithecus, 9 cranial frags reconstructed, 10 lower teeth, 11 upper teeth	Leakey, Tobias, Napier, 1964

Found	Number	Site	Description	Published
1963	OH 17	FLK Maiko Gully	Part deciduous, molar	unpublished
1969	OH 18	FLK	Phalanx of hand	unpublished
1963	OH 19	FC II W	upper molar	unpublished
1959	OH 20	HWK II	? A. boisei prox. shaft and neck, L. femur	Day, 1969
1968	OH 21	FLKN	H. Habilis LM^1	Leakey, Clarke, Leakey, 1971
1968	OH 22	FLKN	cf. H. erectus, R mandible (P_3-M_2)	unpublished
1968	OH 23	FLK IVb	Homo sp. L mandible (P_4-M_2)	unpublished
1968	OH 24	DKE I	Homo sp. restored cranium	Leakey, Clarke, Leakey, 1971
1968	OH 25	Geologic Loc 54, Bed IVa	Frag. left parietal near asterion	unpublished
1969	OH 26	FLK West	RM_3	unpublished
1969	OH 27	HWK I East	H. habilis RM_3	unpublished
1970	OH 28	WK	H. erectus L innominate, L femur	Day, 1971
1969	OH 29	JKW, Beds III - IVa	Frag. molar	unpublished
1969	OH 30	FLK Maiko Gully	Upper teeth: Ldm^{1-2} C-m^1 Rdm^{1-2} C, M^1 Lower teeth: RI_{1-2} LI_1 C, M_1	unpublished
1969	OH 31	HWK EI	broken molar	unpublished
1969	OH 32	MNK II	broken molar	unpublished
1969	OH 33	FLK NNI	vault fragments of skull	unpublished
1962	OH 34	JKW III-IVa	H. sp. femur shaft and part of tibia shaft	unpublished
	OH 35	FLK	H. habilis shaft and distal L tibia	unpublished

Found	Number	Site	Description	Published
	OH 36	SC	cf. H. erectus ulna	unpublished
	OH 37	SC	H. sp. fragment L mandible (M_{1-2})	unpublished
	OH 48	FLK NN I	cf. australo. clavicle	unpublished
	OH 49	FLK NN	cf. australo. radius shaft	unpublished
	OH 50	FLK NN	rib shaft	unpublished
	OH 43		metatarsals	unpublished

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1965 Fission track dating of Bed I, Olduvai Gorge. Science 148: 72-74.

Experimental procedure is outlined and a date from volcanic pumice taken from site DK I is given at 2.03 ± ·28 million years.

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1959 On the basis of Pleistocene correlation in East Africa. Geolog. Mag. 96: 265-284.

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1963 Magnetization of basalt in Bed I, Olduvai Gorge, Tanganyika. Nature 200: 560-561.

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1958 Recent discoveries at Olduvai Gorge, Tanganyika. Nature 181: 1099-1103.

1959a A new fossil skull from Olduvai. Nature 184: 491-493.

1959b The first men; recent discovery in East Africa. Antiquity 33.

1960a Finding the world's earliest man. National Geographic 118: 420-43

1960b The affinities of the Olduvai australopithecine. Nature 186: 458.

Reply to J. T. Robinson (Nature 186: 456-458) concerning the taxonomic status of *Zinjanthropus boisei*. He agrees that *Zinjanthropus* is closely related to the australopithecinae but believes the differences are enough to justify separate generic rank from *Paranthropus*. Claim based on alleged differences in cranium and relatively greater reduction of the canines in comparison with total molar-premolar series.

1961a New finds at Olduvai Gorge. Nature 189: 649-650.

Announces the discovery of additional specimens of fossil hominid at FLK NN I including a hominid mandible as well as parts of two parietals. Age of the specimen estimated at 12 years on the basis of present day tooth eruption. Claims overall dental pattern does not appear to be compatible with *Zinjanthropus.*

1961b The juvenile mandible from Olduvai. Nature 191: 417-418.

Additional information on the mandible of the juvenile hominid discovered at the site FLK NN I (OH 7). Describes the measurements for the third and fourth lower premolars, the first and second lower molars, and a single upper molar Believes the juvenile is a very remote and truly primitive ancestory of *Homo*.

1961c Exploring 1,750,000 years into man's past. National Geographic 120: 564- .

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1963b East African fossil Hominoidea and the classification within this super-family. *In* Classification and Human Evolution, S. L. Washburn (ed.), New York: Aldine Pub. Co., 32-49

1965 Olduvai Gorge, Volume I. New York: Combridge University Press, 118 pp.

1966 *Homo habilis*, *Homo erectus* and the australopithecines. Nature 209: 1279-1281.

> Argues that *Homo habilis* is distinct from any australopithecines in many morphological aspects; the U-shaped structure of the australopithecine mandible being the most obvious. He also believes that by Lower Pleistocene times *H. habilis* *H. erectus*, as well as the australopithecines, were all evolving along distinct lines and rejects the idea that the *H. habilis* represents a stage between *A. africanus* and *H. erectus*.

Leakey, L.S.B. and F.C. Howell

1960 The newest link in human evolution; the discovery by L.S.B. Leakey of *Zinjanthropus boisei*. Current Anthropology 1: 76-77.

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1964 Recent discoveries of fossil hominids in Tanganyika: at Olduvai and near Lake Natron. Nature 202; 5-7 (reprinted in Current Antrhopology 6: 422-424 (1965)).

> Specimens from sites VEK IV (OH 12), MNK II (OH 13), (OH 14), (OH 15); and FLK II Maiko Gully (OH 16) are announced as well as a large australopithecine mandible from Lake Natron by Richard Leakey and Glynn Isaac.

Leakey, L.S.B., Napier, J. R., and Tobias, P.V.

1964 A new species of the genus *Homo* from Oldúvai Gorge. Nature 202: 7-9.

> Revised diagnosis of the genus *Homo* to include a new species *Homo habilis*. Differs from australopithecus in cranial capacity of 600+ cc., and lacks concave or dished-in face with smaller molar teeth. Describes the type specimen OH 7 and paratypes OH 13, 8, 6, and 4 and referred material Oh 14, 16. Claims contemporaneity with *Australopithecus*.

Leakey, M. D.
1969 Recent discoveries of hominid remains at Olduvai Gorge, Tanzania. Nature 223: 756.

The nearly complete skull (Oh 24) from DK East is preliminarily described. The specimen was discovered in the earliest known fossiliferous horizon. Stone tools were found of the Olduway type in a nearby site. The discoveries of OH 21, 22, 23, 26, and 27 are also announced.

1971 Olduvai Gorge, Volume III. Combridge, UK: Combridge University Press.

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1971 New hominid skull from Bed I, Olduvai Gorge, Tanzania. Nature 232: 308-312.

OH 24 is announced from site DKE I, which differs in some respects from the type of *Homo habilis* from Bed I. A case for sexual dimorphism is made. A complete description of the cranium is made as well as comparisons with *Australopithecus* and *Homo erectus*. Claims that the differences which exist between the type *H. habilis* from Bed I and the paratypes from Bed II are not the result of an elapse of a prolonged time interval.

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1970 Early hominids and cranial capacities. Nature 227: 747-748.

On the basis of comparing the cranial capacity of OH 7 with that of other gracile australopithecines, the author does not feel that the specimen should be included in the species *A. africanus* but rather to another species of the same genus. OH 7 differs as much from earlier hominids as does the gorilla from the chimpanzee.

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1965a *Homo habilis* and the australopithecines. Nature 205: 121-124.

1965b Comments on 'New Discoveries in Tanganyika: Their Bearing on Hominid Evolution', by P. V. Tobias. Current Anthropology 6: 403-406.

1966 The distinctiveness of *Homo habilis*. Nature 209: 957-960.

Acknowledges that some detectable differences between known specimens of *Homo habilis* and known australopithecines exist but questions the significance of those differences. Recalculates cranial capacities for australopithecines and gives range between 300-550 cm^3. Reiterates his position of maintaining separate generic rank between *Paranthropus* and *A. africanus* and proposes lumping australopithecines with genus *Homo*.

Simons, E., P. Ettel and D. Pilbeam
1969 Controversial taxonomy of fossil hominids. Science 166: 258-259.

Discusses the position of *Homo habilis*. Claims that the Bed I "habilis" material closely resembles *Australopithecus sp.* from South Africa and that the evidence favors its placement in that genus. The Bed II "habilis" material differs in size from Bed I and resembles *Homo erectus*. Reiterates valid objections to the concept "*H. habilis*" and proposes procedures to be used to assess taxonomic affinities.

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> Defends the validity of the species *Homo habilis*. Examines dental characteristics, inner contour of the mandible, the length/breadth index of molar teeth, and cranial capacity of *Homo habilis* and *Australopithecus*. Recognizes three branches of the australopithecinae, a mesodont branch (*A. africanus*), a macrodont branch (*A. robustus*) and a megadont variant (*A. boisei*).

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> The author supports the assignment of OH 24 to the genus *Homo*, and explains why, despite arguments that uts cranial capacity is too small and its dished face is more characteristic of australopithecines. No plates or tables.

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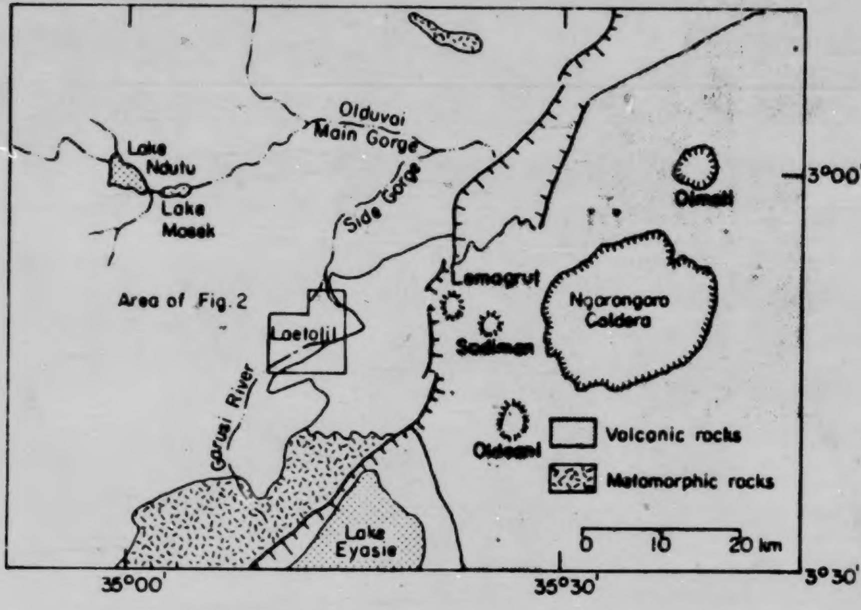
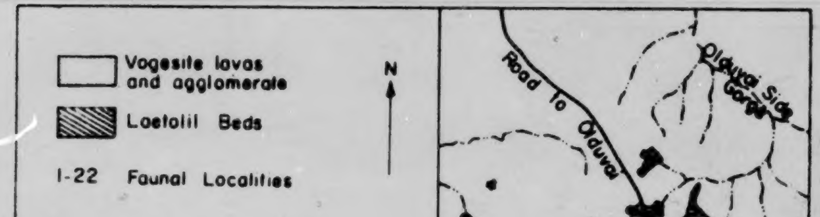
> Reiterates his previous view that OH 7 should be considered as part of the population of South African gracile australopithecines and grouped under the taxonomic rank of *Homo africanus*.

FIGURE 11-14


Olduvai Main Gorge
Side Gorge
Lake Ndutu
Lake Masek
Olmoti
3°00'
Lemagrut
Ngorongoro Caldera
Sadiman
Area of Fig. 2
Laetolil
Garusi River
Oldeani
Volcanic rocks
Metamorphic rocks
Lake Eyasie
0
10
20 km
35°00'
35°30'
3°30'

Site localities
Olduvai Gorge and Laetolil


Vogesite lavas and agglomerate
Laetolil Beds
1-22 Faunal Localities
N
0
1
2
3 km
Road to Olduvai
Olduvai Side Gorge
Gadjingero River
Road
Garusi River
1
2
3
6
7
7 East
8
9 North
9 South
10
10 N-E
10 East
10 West
11
12
13
14
15
16
17
18
19
20
21
22

The Laetolil Beds

Laetolil

The Laetolil locality proper is found in the upper reaches of the Vogel River drainage, however, the Laetolil Beds (Kent 1941) are a fairly extensive series of shallow tuffaceous exposures along the Vogel River and related streams on the plateau above the northwestern margin of the Eyasi Rift valley and below the south westerly slopes of the Lemagrut volcano (Figure 11-14) Laetolil Beds have been traced northward some 35 miles into the Side Gorge at Olduvai where they underlie deposits of Bed I. The sediments were first explored by Kent and Louis Leakey in 1935.

Kent (1941) has described the geology of these deposits along the Eyasi Rift scarp as agglomeratic tuffs and presumed ash flows which may be fossiliferous and reach a maximum recorded aggregrate thickness of nearly 30 meters. He recognized three main subdivisions of the stratigraphic sequence. The lower 15 meters are fine, subaerially deposited tuffs which pass upward into five aeolian tuffs interbedded with tuffaceous clays and pebble bands. The upper part of the sequence is represented by waterlain yellowish - gray tuffs. A basalt layer unconformably overlies these tuffaceous deposits. Kent named the lower unit the Laetolil Beds and the upper the Ngaloba Beds separated from the former by a middle layer of olivine-rich lava flows and agglomerates. These fossiliferous sediments were rediscovered by Ludwig Kohl-Larsen in 1938-39 who also discovered the first hominid remains consisting of a small piece of a left maxilla with two premolar teeth. An additional third molar recovered at some distance from the original find, but attributed to it, may be considerably younger. Dietrich (1942, 1950) has described the fossil vertebrates, including the hominid maxilla, recovered by Kohl-Larsen, and recorded the fossiliferous localities sampled. However no published accounts of the specific stratigraphy at these fossiliferous localities were completed. The hominid specimen was further described by Weinert (1950) and (1951) as Meganthropus africanus. Some further collecting was carried out in 1959 and 1964 under the direction of Louis Leakey.

The deposition of the Laetolil Beds has been reexamined by Hay who concludes that the conditions appear to be largely terrestrial of a steppe-grassland environment based on the vertebrate assemblages which lack aquatic elements and the aeolian tuffs which resemble those of Bed II, Olduvai Gorge.

The age of the Laetolil Beds has generally been given in biostratigraphic terms; most recently by Maglio (1969). In general it was thought that the sediments and their contained fauna were broadly contemporary with Olduvai Bed I or slightly older. As the sediments are interbedded with the Lemagrut lavas they are demonstrably older than the "Basalt" and "Upper Members" of Olduvai Bed I. Maglio (1969) has suggested on comparative biostratigraphic grounds that at least two faunas have been sampled and that the age of these faunas lie between 2 and 4.0 m.y. Recent work on the mammalian fauna has shown that rodents are fairly well represented although not abundant. The most common faunas are Pedetes, Saccustomus and Hystrix. The carnivore fauna is well represented by viverrids, hyaenids, filids, and one machairodont. Proboscidea include Deinotherium and Loxodonta sp.; equids consist of the single genus Hipparion; suids include both Potamachoerus and Notochoerus; rhinocerotids are represented by both Ceratotherium and Diceros; giraffids, by Sivatherium and Giraffe jumae; and bovids, by a high percentage of Madogua.

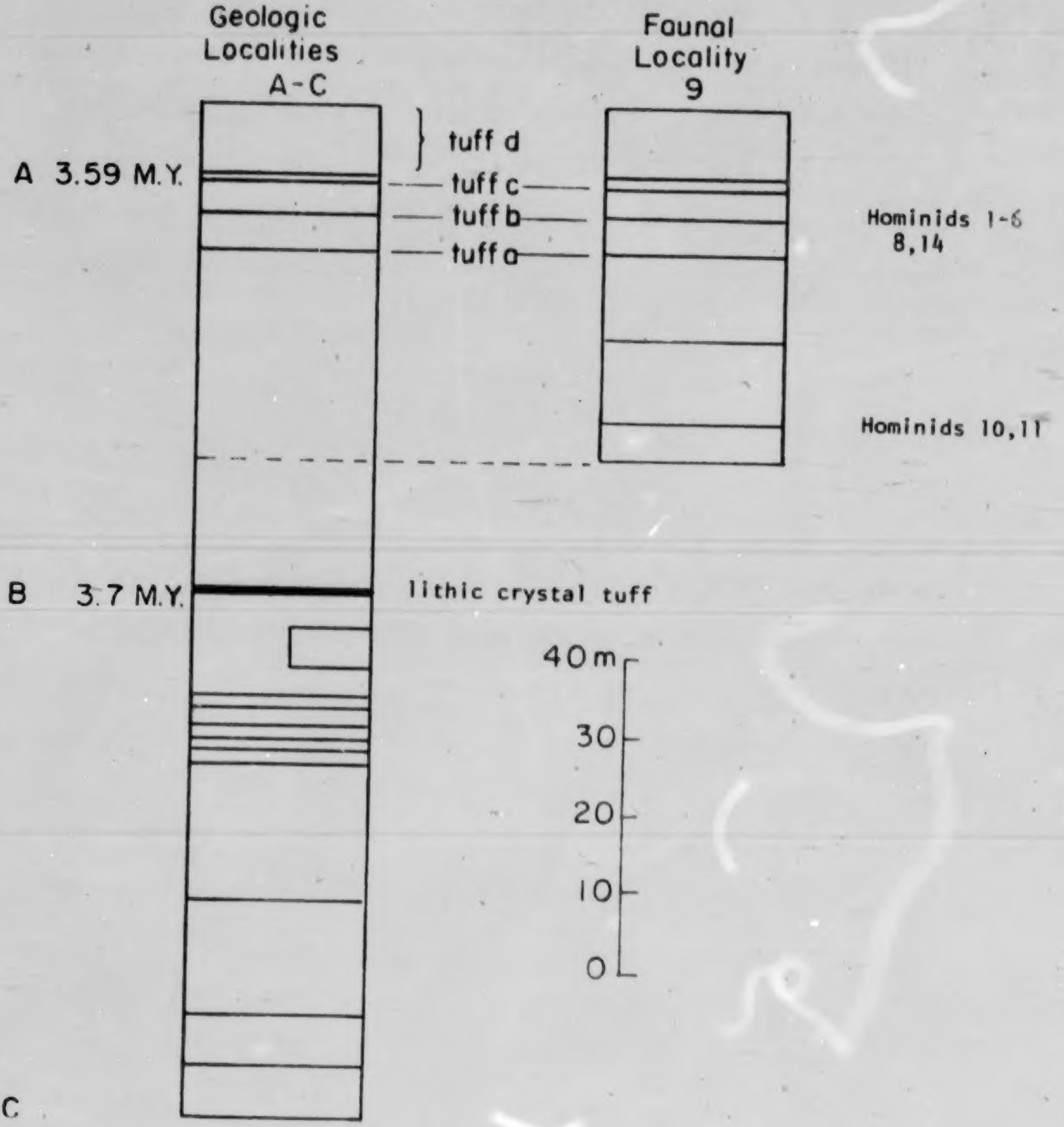
Interest in the area was renewed in 1974 when several herbivore teeth were recovered above Lake Masek in exposures of the Laetolil Beds. The fauna recovered included a single hominid premolar.

Subsequent work on the geology of the area demonstrated that the Laetolil Beds were formed during the eruptions of the Sadiman Volcano, and are considerably more extensive than previously believed, some 130 m in thickness in an area incompletely exposed. The exact extent is unknown. The 130 meter section is divisible into an upper half of aeolian tuff and the lower half of interbedded ash-fall and aeolian tuff with minor conglomerates and breccia.

Hominid remains and nearly all of the other vertebrates are confined to the uppermost 30 m of aeolian tuffs. (Figure II-15). Within the upper unit there are three prominent marker tuffs designated a,b,c, which can be used for correlating within the sediments. The whole sequence is capped by tuff d. An erosional surface separate tuff d and the underlying aeolian tuffs from additional fossiliferous sediments which may or may not be part of the Laetolil Beds. Sediment deposits representing Beds I and II at Olduvai lie within the stratigraphic sequence between the overlying (vogesite) lavas of the Lemagrut Volcano (2.38-2.43 ± .5 m.y.) and the uppermost Ngaloba Beds.

Recent potassium argon dates of the tuffs lying within the Laetolil Beds have yielded age determinations from tuff c and xenolithic horizons underlying tuff c which average 3.59 m.y. Additional dates from tuffs some 50 meters below tuff c (see stratigraphic column Figure II- 15) at locality B average 3.77 m.y. and give the lower limit to the age of the hominid remains.

FIGURE 11-15


Geologic Localities A-C
Faunal Locality 9
tuff d
A 3.59 M.Y.
tuff c
tuff b
tuff a
Hominids 1-6 8,14
Hominids 10,11
B 3.7 M.Y.
lithic crystal tuff
40m
30
20
10
0
C

GEOLOGICAL COLUMN OF THE LAETOLIL BEDS

The original hominid material is thought to be contemporaneous with that of the other fossil vertebrates. The coloration of the remains has been interpreted by Maglio to indicate an older time interval represented in the Laetolil sequence. Since 1974-75 thirteen new fossil hominids have been recovered by Mary Leakey and include a single maxilla, several mandibles and isolated teeth, and are confidently associated to the Laetolil Beds.

Compared to other East African remains of comparable dates the Laetolil anterior dentition appears to be large and the postcanine teeth, small to moderate in size. Both deciduous and permanent dentition is represented.

The deciduous canines are slightly projecting and sharply conical in shape. In overall morphology it is similar to the permanent canine. Adult mandible (LH 4) shows that the dental arcade is essentially undistorted and presents straight sides which converge anteriorly. The P_3 shows some wear on the buccal surface and a diastema exists for the tip of the upper canine.

The sample of the hominid remains seems to represent a single phylogenetic lineage. The dentition resembles closely the hominid specimens from Sterkfontein, and certain specimens from East Rudolf (ER #820, 1507) as well as the recently discovered material from the Afar. Recent assessments stress the similarity to later members of the genus Homo and according to M. Leakey et al. (1976) the Laetolil specimens should be placed as earlier members of that genus.

Laetolil Fossil Hominids

Described Leakey, M. et al. 1976

Date	Site	Number	Description
1974-75	1	1	R p^4 fragment
	3	2	immature mandibular corpus
	7	3 a-t	isolated deciduous and permanent teeth
	7	4	adult mandible and dentition
	8	5	adult maxillary row $I^2 - m^1$
	7	6 (a-e)	Isolated upper teeth
	5	7	Rm$^{1\ \mathrm{or}\ 2?}$
	11	8	Rm^2, Rm^3
	10W	10	left mandibular corpus
	10w	11	Lm$^{1\ \mathrm{or}\ 2\ ?}$
	5	12	Lm$^{2\ \mathrm{or}\ 3\ ?}$
	8	13	right mandibular corpus fragment
	19	14	Isolated lower permanent teeth

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H. Weinert
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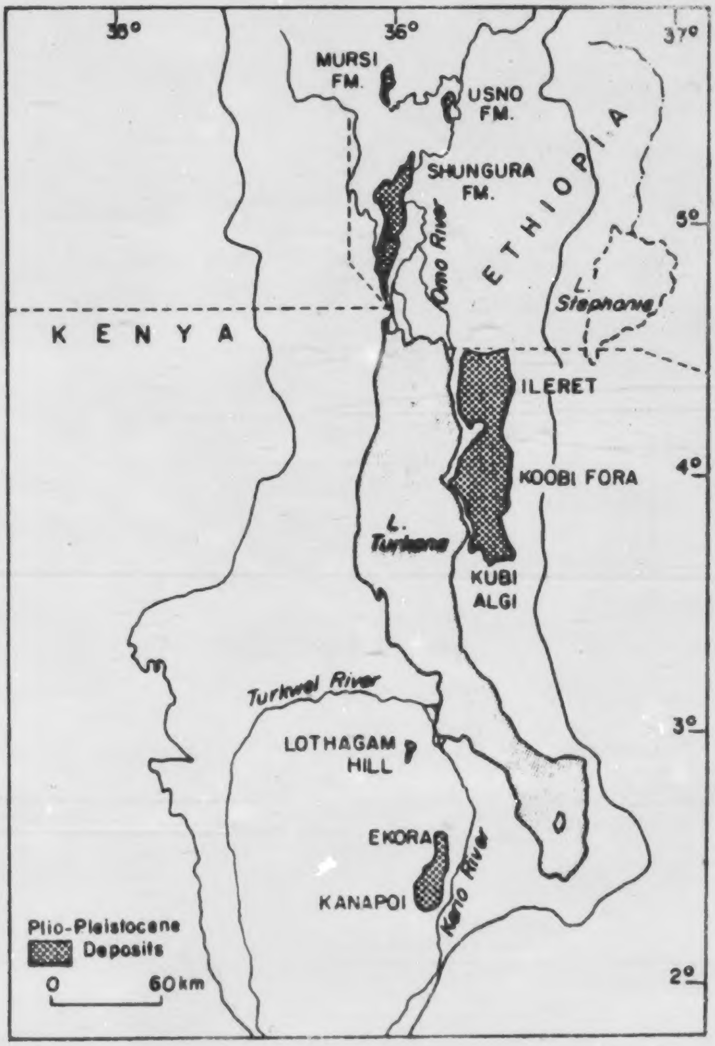
AREA III

Northwestern Kenya
Lake Turkana Basin

- Kanapoi
- Ekora
- Lothagam Hill
- Lower Omo Basin
- Ileret
- Koobi Fora
- Kubi Algi

FIGURE 11-16

Distribution of the Principal Hominid Sites in the Lake Turkana Basin, Ethiopia and Kenya


35°
36°
37°
MURSI FM.
USNO FM.
SHUNGURA FM.
Omo River
ETHIOPIA
5°
L. Stephanie
KENYA
ILERET
KOOBI FORA
4°
L. Turkana
KUBI ALGI
Turkwel River
3°
LOTHAGAM HILL
EKORA
KANAPOI
Kerio River
Plio-Pleistocene Deposits
0 60km
2°

Rudolf Basin

In 1975 the name of Lake Rudolf was changed to Lake Turkana by a decree of President Kenyatta of Kenya. Such changes in place names for most geographical features would hardly be noteworthy to paleoanthropologists if it were not for the demonstrated importance of the area to the discipline which has stretched back through 70 years of research.

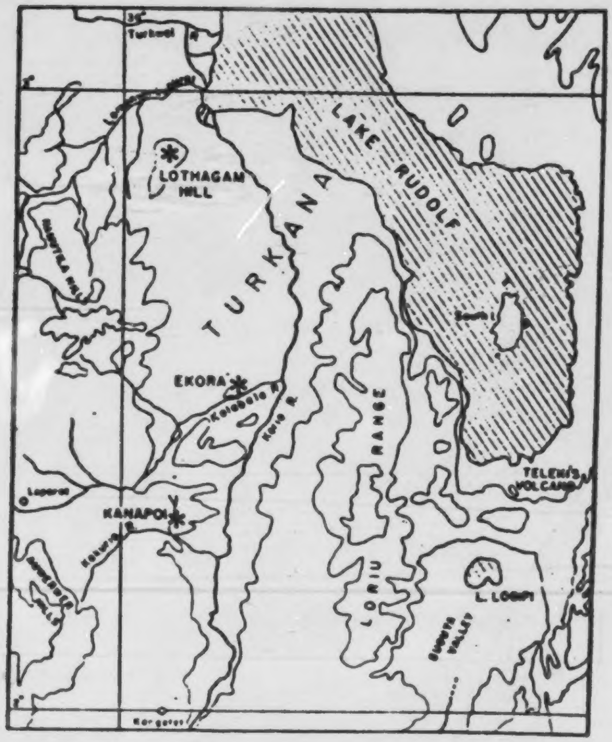
The earliest accounts of the rich geological history of the Rift Valley were published by Joseph Thomson (1881). However, it was not until 1902 that neogene fossils were first recovered in the Lake Turkana Basin in southwestern Ethiopia. More systematic work by Arambourg in 1933 determined the beginnings of the geological successions and resulted in the publication of a large paleontological inventory. At the same time the first substantial effort to record the natural history and geology of the western margin of the lake was attempted by the Cambridge expedition led by F. Worthington in 1930-31. Further geological studies to the west, south and southeast were carried out by the Rudolf Rift Valley expedition led by V. Fuchs in 1934. More extensive geological investigations were crried out by Sir Frank Dixey in the Northern Frontier District and Turkana in 1943. Again concentrating along the western margin in North Turkana during the late 1950's T. Whitworth continued the paleontological and geological researches. Archeological investigations were not undertaken until the mid-sixties when L. H. Robbins began his work in South Turkana.

The more recent round of paleoanthropological investigations were instigated by Louis Leakey who, in 1964, interested Harvard University and Bryan Patterson in exploring parts of the area to the southwest of the lake.

south of the Kerio Valley in South Turkana. This work was continued in 1968 by Vincent Maglio followed in 1971 by David Kinsman as coordinator of the present geological and paleontological work.

Detailed studies of the Omo began in 1967, with the encouragement of the late Emperor Haile Sclassie, by the Omo Research Expedition sponsored by the University of Chicago, the Musee de l'Homme and the National Museums of Kenya. The American team led by F.C. Howell recorded the extensive Shungura deposits from 1968 to 1974. Up until the death of C. Arambourg in 1969 and thereafter until 1974 under the direction of Y. Coppens, the French group directed their efforts to the South of Shungura. The Nairobi group led by R. Leakey spent one season in the Omo and then shifted their efforts to the eastern side of Lake Turkana, in Kenya and have researched this area since 1968.

FIGURE II- 17


Turkwel R.
LOTHAGAM HILL
TURKANA
LAKE RUDOLF
South I.
EKORA
Kalabata R.
Kerio R.
LORIU RANGE
TELEKI'S VOLCANO
KANAPOI
L. LOGIPI
SUGUTA VALLEY

Map of the Southwest Lake Rudolf hominid bearing deposits of Lothagam, Kanapoi and Ekora localities, Kenya.
(From Patterson et. al. (1970):919)

SOUTH WEST LAKE RUDOLF

Three localities of Pliocene/Pleistocene age are located in the Turkana district, Southwest Lake Rudolf, a large basin drained by the Kerio River. Two of the localities, Kanapoi and Lothagam, have yielded hominid fossils in association with assemblages of other vertebrates collected by the Harvard expedition of 1966-67. The third locality, Ekora, has not as yet produced fossil hominid remains. Kanapoi and Ekora are adjacent localities lying to the south of Lothagam Hill.

The Kanapoi sediments are exposed by dissections of the Kakurio River, a seasonal tributary to the Kerio. The sediments overlie a Miocene surface, are some 65-70 meters in thickness, and are fluviolacustrine in content. Interbedded successive ash falls and substantial deposits of waterlaid tuffs are present. Three initial radiometric age determinations on an overlying basalt member earlier published produced an average minimum age of the Kanapoi sediments of 2.7 m.y. Geomagnetic determinations of the lava showed reversed polarity. Subsequent redating of the basalt member based on reports of contamination, has yielded ages between 4 and 4.5 m.y. These dates correlate closer with the fauna which is comparable to that of the substantially older Mursi fauna at the Omo. The single hominid specimen (Kanapoi Hominid 1), represented by the distal end of the left humerus, is therefore of particular interest as the oldest of such remains from this period.

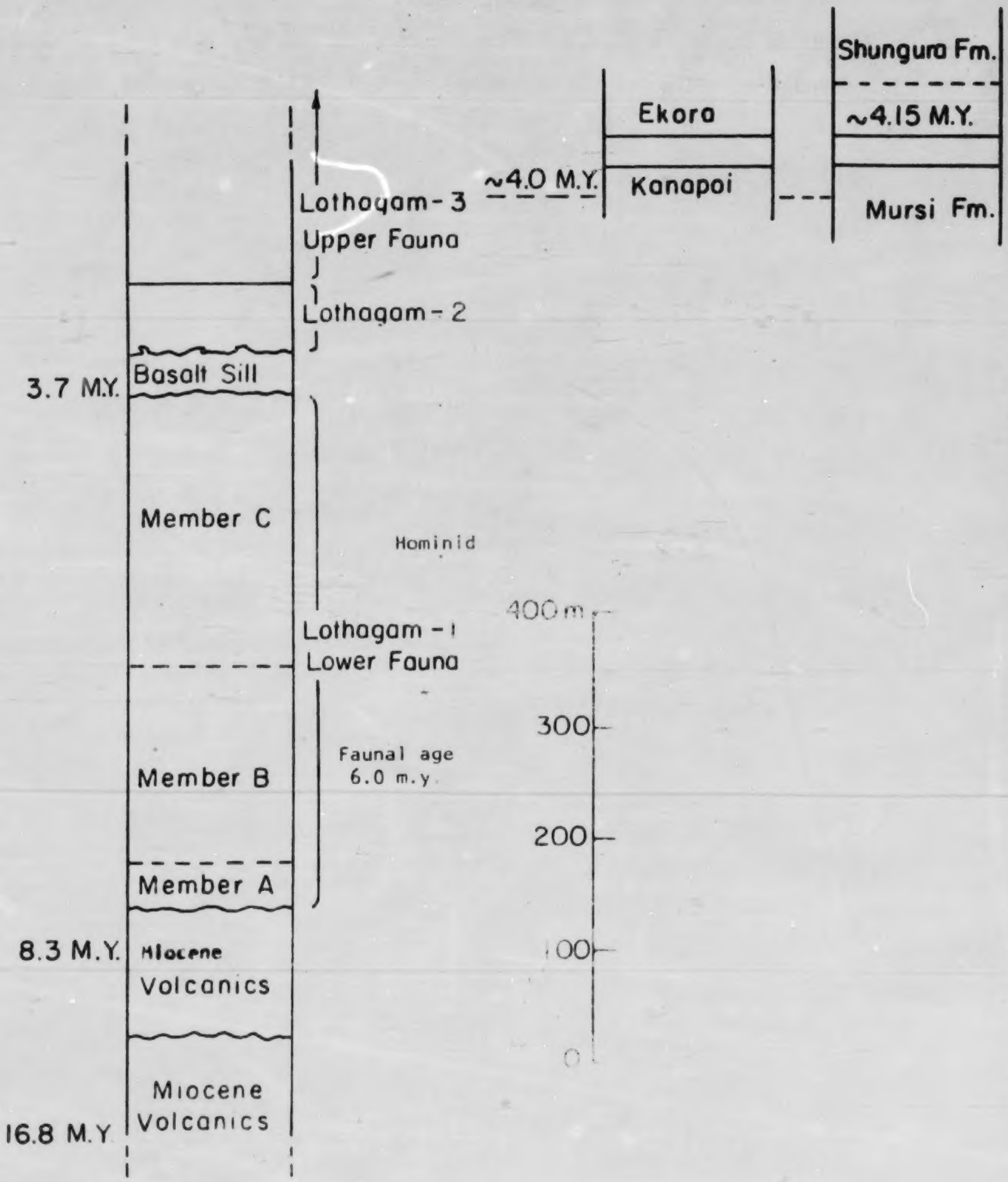
The Ekora sediments are less well known than those from Kanapoi or Lothagam primarily because they are poorly exposed. The sediments overlie a basalt which is assumed to be continuous with that overlying the sediments from Kanapoi (Patterson *et al*. 1970)

The faunas from Kanapoi and Ekora are essentially contemporaneous (Behrensmeyer 1976) and indistinguishable from that of Lothagam 3 (Maglio 73:69) both yielding an indicated age of 4.0 m.y. The Ekora fauna would thus be slightly younger than 4.0 m.y. since it is derived from sediments lying avove the Kanapoi Basalt.

To the northeast of Kanapoi, the Lothagam Hill locality represents isolated exposures of Miocene and Pliocene volcanics dated radiometrically between 16.8 and 8.3 m.y. overlain by Late Tertiary sediments. The Lothagam Group totals over 700 meters in thickness and three principal sedimentary units, Lothagam 1-3, have been recognized. Early paleontological and geological work was began by Bryan Patterson of Harvard University in 1967. Additional explorations and geological investigations were undertaken by Maglio and Behrensmeyer in 1968. This work has continued since 1972 by investigators V. Maglio, and more recently C. Smart and D. Powers from Princeton University.

Lothagam I is subdivided lithologically into three members, A (the lowest stratigraphically), B, and C. Member A consists of nonfossiliferous conglomerates and sandstones deposited in alluvial and fluvial environments. Member B is primarily of sandy-silts and thinner conglomerates possibly representing periods of cyclic sedimentation under fluvial and fluvio-deltaic conditions. Member B is overlain by the laterally continuous "red marker bed" and overlying pink agglomeritic tuff which has yiedled no consistent K-Ar dates. Member C consists of fluvially deposited channel and overbank facies. All of the fossil assemblage constituting the "lower fauna" has been recovered from members B and C. The lower

FIGURE II - 18


Shungura Fm.
~4.15 M.Y.
Mursi Fm.
Ekora
Kanapoi
~4.0 M.Y.
Lothagam-3
Upper Fauna
Lothagam-2
Basalt Sill
3.7 M.Y.
Member C
Hominid
Lothagam-1
Lower Fauna
Faunal age
6.0 m.y.
Member B
Member A
8.3 M.Y.
Miocene
Volcanics
Miocene
Volcanics
16.8 M.Y.
400 m
300
200
100
0

GEOLOGICAL COLUMN OF THE LOTHAGAM GROUP, EKORA AND KANAPOI fauna estimated from 5.0 to 5.5 m.y. (Patterson *et al*. 1970) is distinctly older than that of the younger fauna of Lothagam 3.

Deposition of the sediments of Lothagam 2 occured under lacustrine conditions intervening between the fluvial phases of Lothagam 1 and 3.

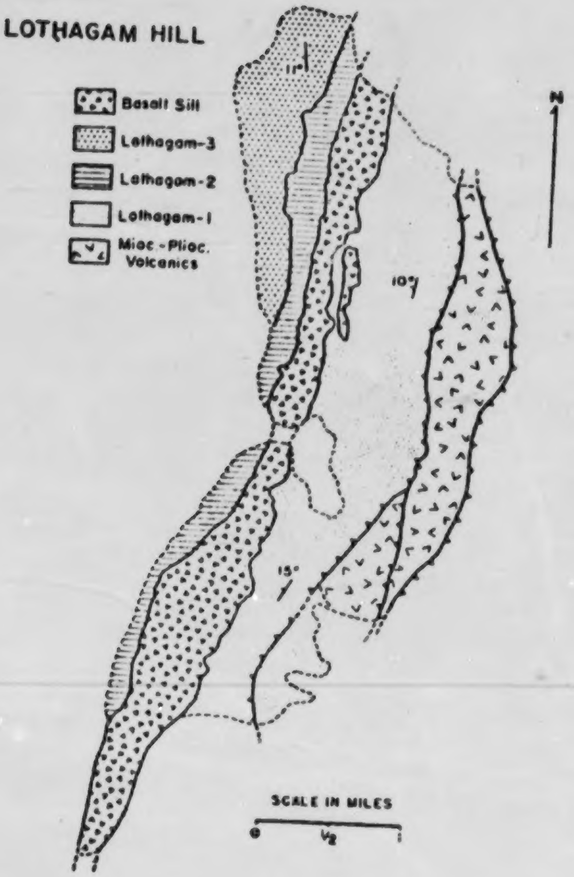
The Lothagam group rests on lavas dated 8.3 ± .25 m.y. and is presumably older than 3.73 ± .41 m.y., the age of the overlying intrussive basalt sill. Reworked tuffaceous units within the sequence show little possibility of yielding additional reliable dates. (Behrensmeyer 1976). Faunal ages for the vertebrate remains is based on work completed on the Proboscidea by Maglio (73.20) who has compared the molars of *Stegotetrabelodon orbus* from Lothagam I with samples from the Kaparyon beds (5.0 m.y.) and the Mpesida beds (7.0 m.y.) from Baringo. Recent work on *Hipparion* has indicated an age for the Lothagam IB fauna to be somewhat older than 6.0 m.y. (Hooijer and Maglio 1974). The nonmammalian portion of the fauna list especially the geese and fish reflects the depositional environment indicated by the sediments themselves. The mammalian component indicates that two main habitat types occured nearby. Both gallery forest forms such as *Cercocebus* and savannah forms such as *Hipparion turkanense* occur simultaniously (Smart 1976).

The younger fauna of Lothagam 3 is sparce but correlates with that from the Mursi Fm. and lower Shungura of the Omo Group, the Kubi Algi Fm of East Rudolf and the Chemeron Fm. in the Baringo succession (Behrensmeyer 1976). The indicated age is about 4.0 m.y.

The single hominid specimen from Lothagam I together with other vertebrate fossils were recovered during the field investigations of the Museum of

Comparative Zoology, Harvard University during 1967. The mandible was a surface find eroded out of the upper half of member C. The hominid specimen was described as Australopithecus sp. cf. A. africanus and consists of a fragment of the mandibular body with worn M_1, perhaps the oldest known fossil representative of the family Hominidae.

Figure 11-19


LOTHAGAM HILL
Basalt Sill
Lothagam-3
Lothagam-2
Lothagam-1
Mioc.-Plioc. Volcanics
11°
10°
15°
N
SCALE IN MILES
0
½
1

Simplified geological map of Lothagam locating deposits listed in columnar section.
(From Patterson et. al. (1970):919)

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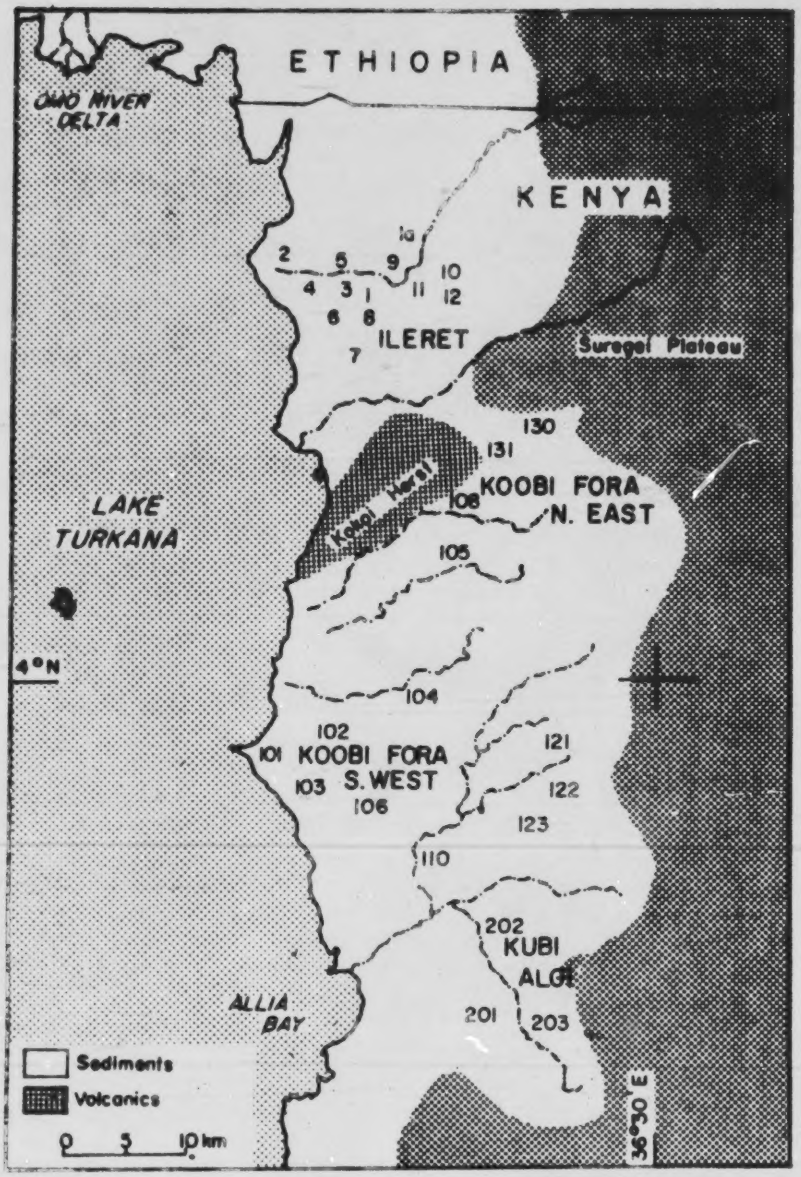
FIGURE 11-20


ETHIOPIA
OMO RIVER DELTA
KENYA
1a
2
5
9
10
4
3
1
11
12
6
8
ILERET
7
Suregei Plateau
130
131
KOOBI FORA N. EAST
108
Kokoi Horst
LAKE TURKANA
105
4°N
104
102
101
KOOBI FORA S.WEST
103
106
121
122
123
110
202
KUBI ALGI
ALLIA BAY
201
203
Sediments
Volcanics
0 5 10 km
36°30' E

EAST LAKE TURKANA, KENYA

DISTRIBUTION OF PRINCIPAL LOCALITIES

6

EAST LAKE RUDOLF

Geochronology

Located at the northern end of the Kenya Rift system the eastern region of the Rudolf Basin, is comprised of a series of sediments and lavas of Pliocene/Pleistocene age which have been explored since 1968 by investigation teams led by R.E.F.Leakey. Geologic investigations of the area were initiated by A.K. Behrensmeyer in 1969, followed in 1970 by workers from Iowa State University who established and mapped the fundamental rock units. The Basin is delimited on the northeast and east margins by the Suregei cuesta (Plateau) and the sedimentary exposures rest unconformably on Miocene volcanics yielding K-Ar dates of 11.6 ± .5 m.y. These exposures extend south from the Ileret sector to the Koobi Fora and Kubi Algi sectors near Allia Bay and are limited in their southermost extension by a series of varied Pliocene volcanics, Sibilot, Kubi Algi and Derati, and Shin. In total the East Rudolf Basin is in excess of 2500 km^2 and some 325 m in thickness. The Ileret and Koobi Fora sectors are separated by the Kokoi Horst in the west and by Holocene floodplain deposits in the east. Additional Holocene floodplain deposits separate the Kubi Algi sector from the others. The sediments consist of fluvial, deltaic transitional to lacustrine, and lacustrine sediments which are tilted to the west and cut by parallel faults producing eastern facing fault scarps similar to the situation affecting the Usno and Shungura Formations of the Lower Omo Basin to the northwest.

Previous to the identification of continuous marker beds in the sediments . The three sectors in the East Rudolf Basin were referred to by two sets of stratigraphic terms (Figure II-21) from Howell, 1971) Figure II -22) shows the current stratigraphic nomenclature developed after the establishment of geologic correlations between the different sectors (Bowen and Vondra 1973; Vondra and Bowen 1976).

Kubi Algi Formation

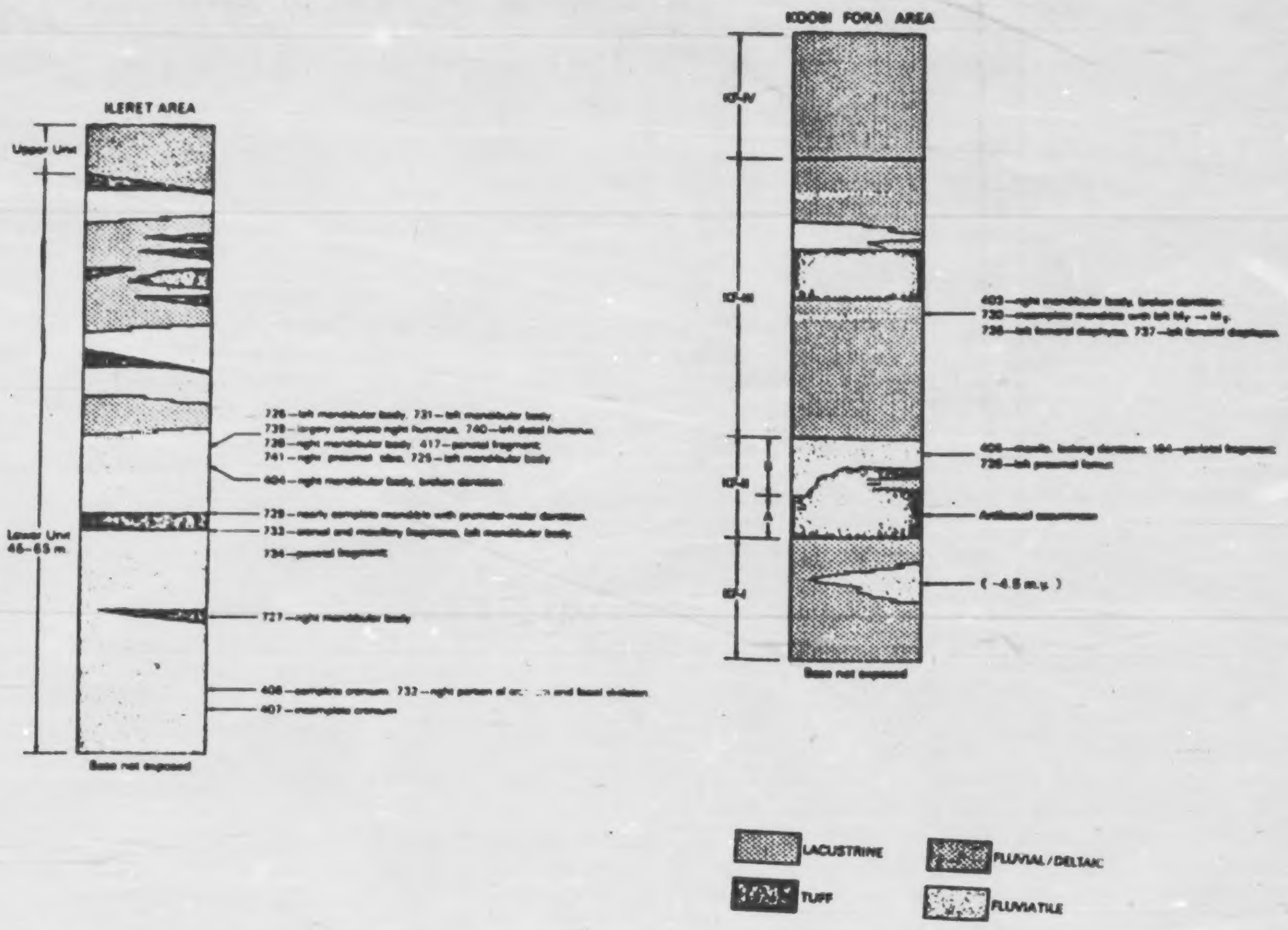
Strata of Pliocene age which overlie unconformably basal Miocene/ Pliocene volcanics and are overlain by Plio/Pleistocene sediments were designated the Kubi Algi Fm. by Bowen and Vondra (1973). The Strata consists of a graded sequence of pebble conglomerates with large cut and fill structures to more fine laminated claystones at the top, deposited essentially in fluvio-deltaic conditions. The sequence is marked at its uppermost boundary by the Suregei Tuff complex. The Formation is 90 m in thickness at the type locality 20 km to the east of Allia Bay. The Kubi Algi Formation is equivalent to the lower deposits in the Koobi Fora and Ileret sectors previously designated as Koobi Fora I. The Pliocene age of the Formation is based on faunal analysis (Maglio 1972) and by associated K-Ar dates ranging from 3.8 to 4.9 m.y. (Fitch and Miller 1976).

Koobi Fora Formation

Sediments comprising the Koobi Fora Formation overlie the Suregei Tuff complex and are overlain by the prominent Chari Tuff which is exposed along the Ileret ridge, and additionally by Holocene lacustrine siltstones (Bowen and Vondra 1973). The type locality was designated near the Koobi Fora Spit. The formation, as it is now defined, includes units of the upper sediments of Koobi Fora I, and Koobi Fora II and III previously designated

FIGURE 11-21

Earlier Stratigraphic Nomenclature of the East Lake Rudolf Succession


ILERET AREA
Upper Unit
Lower Unit 45–65 m
726—left mandibular body. 731—left mandibular body
739—largely complete right humerus. 740—left distal humerus
728—right mandibular body. 417—parietal fragment
741—right proximal ulna. 725—left mandibular body
404—right mandibular body, broken dentition
729—nearly complete mandible with premolar-molar dentition
733—cranial and maxillary fragments, left mandibular body
734—parietal fragment
727—right mandibular body
406—complete cranium. 732—right portion of cr... and facial skeleton
407—incomplete cranium
Base not exposed
KOOBI FORA AREA
KF-IV
KF-III
KF-II
KF-I
403—right mandibular body, broken dentition
730—incomplete mandible with left M1—M3
736—left femoral diaphysis. 737—left femoral diaphysis
405—maxilla, lacking dentition. 164—parietal fragment
738—left proximal femur
Artifactual occurrence
(~4.5 m.y.)
Base not exposed
LACUSTRINE
FLUVIAL / DELTAIC
TUFF
FLUVIATILE

Simplified stratigraphy and hominid bearing localities in the East Lake Rudolf area. From Howell (1971): 344-345.

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by Behrensmeyer (1970) and Vondra et al. (1971), (=Lower and Upper Members) and the lower unit at Ileret (Vondra et al. 1971), (=Ileret Member).

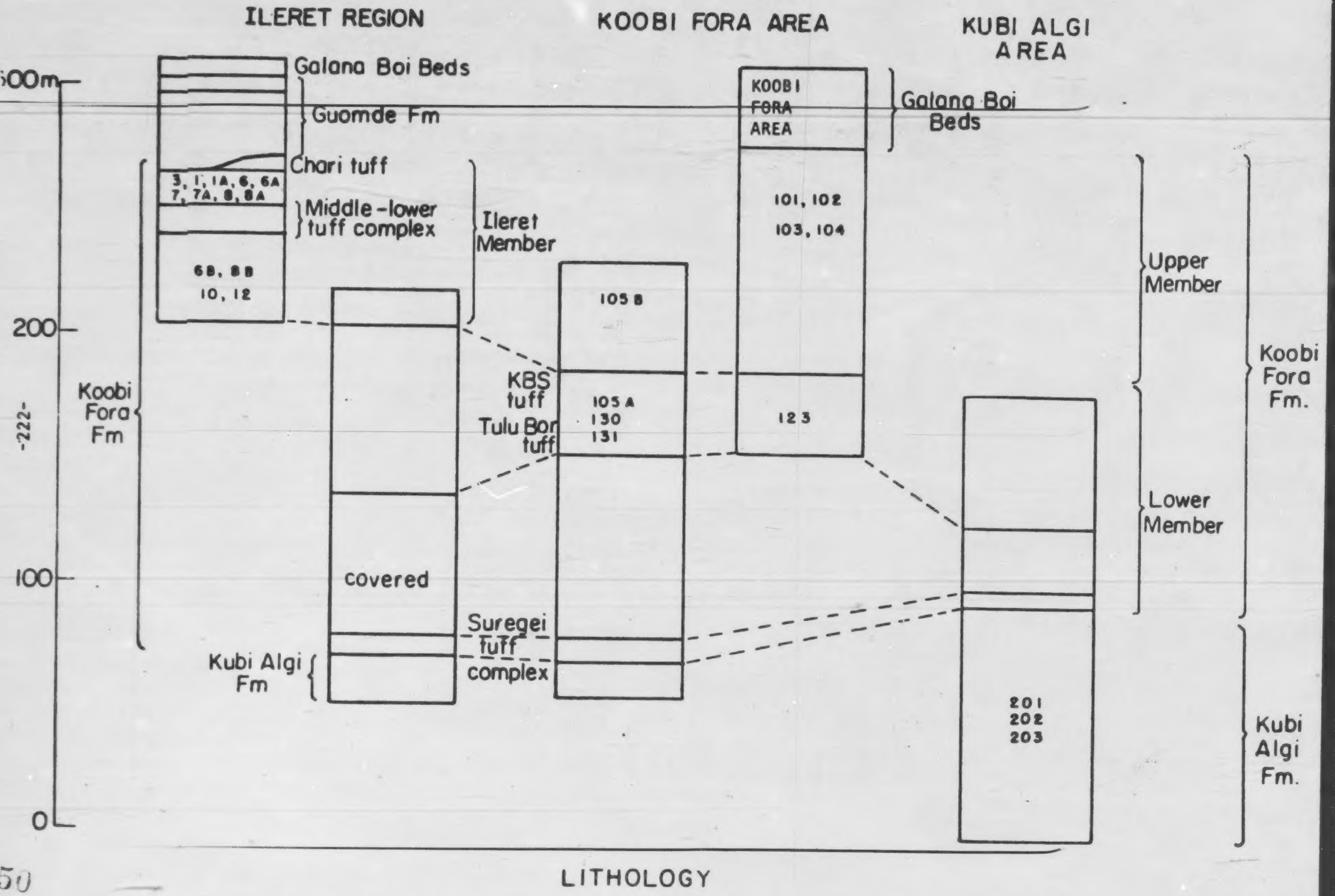
The Lower Member consists of sediments of siltstones, claystones, sandstones and molluscan limestones lying below the KBS Tuff of an Aggregate thickness of 140 m. of the four major lithofacies recognized, the Lower Member is comprised almost entirely of laminated siltstone deposited in a lacustrine environment (Vondra and Bowen 1976).

The Upper Member is comprised of sediments lying above the KBS Tuff in the Koobi Fora sector and below deposits of Holocene age (^{14}C dates range from 9,880 - 4,390) named the Galana Boi Beds. These sediments consist of fluvially deposited conglomerates and mudstones which grade into finer-grained sandstones, siltstones and tuffs, cropping out along the Kakari and Koobi Fora ridges to a maximum thickness of 90 m.

The Ileret member consists of beds in the Ileret sector which lie between the KBS Tuff at the bottom and capped by the Chari Tuff for a total of 66 m in thickness. Individual beds of the Ileret member have not yet been traced to the Koobi Fora sector, however the Chari Tuff based on the radiometric dates (Fitch and Miller 1976) can be equated with the Karari Tuff and possibly the thick Koobi Fora Tuff (Cerling 1973; Vondra and Bowen 1976).

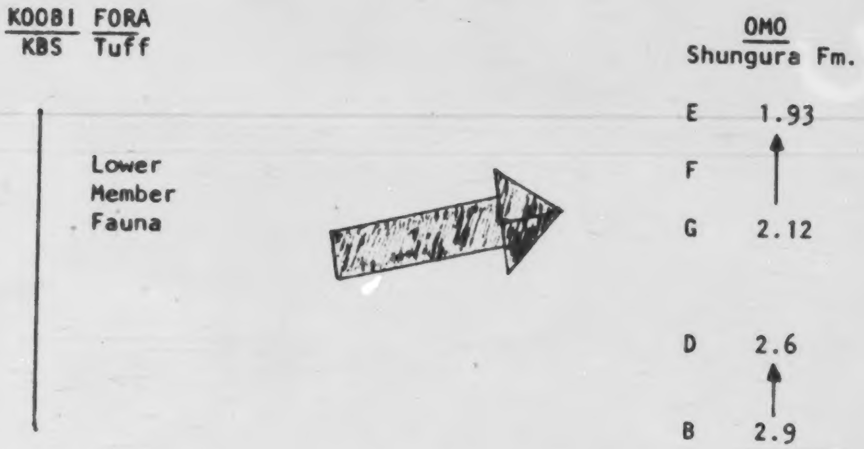
Sediments of predominently lacustrine deposition which overlie the Chari Tuff in the Ileret sector are designated the Guomde Formation. These sediments which were previously referred to as the "middle unit" at Ileret lie below an unnamed thin tuff and the Galana Boi beds.

FIGURE 11-22


ILERET REGION
KOOBI FORA AREA
KUBI ALGI AREA
00m
200
100
0
Galana Boi Beds
Guomde Fm
Chari tuff
3, 1, 1A, 6, 6A
7, 7A, 8, 8A
Middle-lower tuff complex
Ileret Member
6B, 8B
10, 12
Koobi Fora Fm
covered
Suregei tuff complex
Kubi Algi Fm
105 B
KBS tuff
105 A
130
131
Tulu Bor tuff
KOOBI FORA AREA
Galana Boi Beds
101, 102
103, 104
123
Upper Member
Lower Member
Koobi Fora Fm.
201
202
203
Kubi Algi Fm.
LITHOLOGY

The most recent radiometric age determinations of tuffaceous material from East Rudolf have, not surprisingly, shown that the sedimentary sequence is younger than previously believed. Biostratigraphically the lower fauna (=*M. limnetes* zone) recovered from below the KBS Tuff bears strong similarity with the faunas of Members E, F and G (2.12 - 1.93 m.y.) of the Shungura Formation in the lower Omo Basin. If the original radiometric dates of the KBS tuff are correct the lower fauna should bear closer resemblance to that of the older Members B and D (2.9 - 2.6 m.y.).

Figure II - 23



Earlier explanations for this discrepancy between geophysics and paleontology suggested the existence of spatially and ecologically differentiated faunas in these adjacent but environmentally different areas.

Within the stratigraphic sequence several rhyolitic, predominantly reworked, tuffs have served as marker beds for calibration of fossil material. The new Potassium-Argon determinations within the Koobi Fora Formation range from 3.18 m.y. (Tulu Bor Tuff) to 1.22 m.y. for the Chari/Karari Tuff. The original K-Ar determination for the KBS Tuff (type site area 105) was assigned an age of 2.61 ± 0.26 m.y. from a range of widely scattered age determinations (Fitch and Miller 1976; Fitch, Findlater, Watkins and Miller 1974). According to Curtis, Drake, Cerling and Hampel (1975) contamination by older material during the reworking of the tuffs accounts for dates on the older range of the scattering, while subsequent alteration and partial loss of radiogenic argon may explain the younger dates. Curtis *et al*. (1975) further criticized both the methodology and fundamental premises upon which the earlier dates were derived.

The new age determinations were made on samples from the KBS Tuff from three localities yielding consistent dates. Three samples from area 105 and one from area 10 (Ileret) gave an average age of 1.60 ± .05 m.y., while two additional samples from area 131 (Karari Ridge) gave an average age of 1.82 ± 0.04 m.y. The restricted clustering of these new dates strongly suggests that the tuff in area 131 is distinguishable from the KBS Tuff in area 105 and area 10. Additional laboratory analysis have indicated the tuff in area 131 is composed of two pumices, of the same age, but most likely having their origin from two different eruptive sources. The possibility thus arises that older pumices may also be present in the KBS Tuff horizon which might account for the 2.61 m.y- date earlier reported (Curtis *et al*. 1975: 398).

EAST LAKE RUDOLF

Biochronology

More than 133 hominid specimens have been recovered from the exposures of the East Rudolf Basin. Figure II-20 shows the geographic distribution of the collecting localities yielding fauna and artifacts. The three subregions which have been recognized - Kubi Algi (Loc. nos. 200-299), Koobi Fora Ridge (Loc. nos. 100-199), Ileret (Loc. nos. 1-99).

An abundant vertebrate fossil assemblage has been collected along with the hominid remains. Several taxa are represented by successive grades of a single evolving lineage and are, therefore, useful for faunal correlation. The three most important species for this purpose are the suids, Mesochoerus limnetes and Metridiochoerus andrewsi, and the elephant Elephas recki. The faunal samples from the East Rudolf deposits have been divided into four assemblages each based on a distinct group of fossil vertebrates, and each being derived from a definable segment of the stratigraphic sequence. Faunal lists are given in Figure II-24. Biostratigraphic units are correlated with the rock units in Figure II- 22

The mean value of samples from the Mesochoerus limnetes faunal zone can be compared with material from Member F of the Shungura Formation (Tuffs D-F) in the Lower Omo dated radiometrically at about 2.0 million years. The chronostratigraphic limits are 2.7 m.y. and 1.8 m.y. and may be taken as the approximate maximum and minimum indicated age limits for the fauna of the Mesochoerus limnetes zone for this species only. Similar indicated mean and maximum age limits for the Metridiochoerus andrewsi and Loxodonta africana zones are 1.7 m.y. (1.8 - 1.6 m.y.) and 1.2 m.y. (1.4 - 0.9 m.y. respectively (Maglio 1972: 384). Comparing, the elephants' and suids' mean indicated ages and suggested limits from the *M. limnetes* zone are 2.5 m.y. (3.4 - 2.1 m.y.); from the *M. andrewsi* zone are 1.7 m.y. (2.1 - 1.4 m.y.); and from the *L. africana* zone are 1.4 m.y. (1.7 - 1.2 m.y.).

The faunal evidence suggests that the total span of time represented at East Rudolf ranges from 4.5 m.y. to approximately 1.3 m.y. The oldest fauna assemblage, the *N. capensis* zone, correlates with the assemblages from the Mursi (Omo) and Kanapoi Formations. The *M. andrewsi* zone fauna compares well with faunas from Olduvai Bed I and lower Bed II, both younger than 1.85 m.y. However, comparisons of the *Loxondonta africana* zone are not well established though appear to be older than Bed IV Olduvai suggesting that the inferred age of 1.3 m.y. is relatively accurate.

Fossil hominid material has been collected since 1968. By September 1973, these fossiliferous localities had yielded 110 hominid specimens the great majority of which were surface discoveries. For most of these surface specimens the stratigraphic provenance could be determined.

Specimens attributed to *Australopithecus* have been recovered from localities throughout the Koobi Fora Formation and Ileret Member. A range of variation in size has been reported, however, R. Leakey (1976b) believes that they all represent a single species of *Australopithecus boisei*. Size variability has been attributed to sexual dimorphism. Large craniums, such as KNM-ER 406, reveal sagittal and nuchal cresting; more gracile craniums, such as KNM-ER 407 and 732 show no indication of such crests. Other skulls such as KNM-ER 1805 recovered from the BBS Tuff display cresting but have relatively small teeth and small mandibles. This specimen

Figure 11-24

Faunal zone	Areas of occurrence	Geological unit	Diagnosis
Loxodonta africana zone	1, 1A, 3, 6, 7, 7A, 8, 8A	Ileret Member, Koobi Fora Formation	*Elephas recki* stage 3–4 *Loxodonta africana* *Mesochoerus limnetes* (very progressive) *Metridiochoerus andrewsi* (progressive) *Hippopotamus* cf. *amphibius* *Ceratotherium simum* (very progressive)
Metridiochoerus andrewsi zone	6A, 8B, 10, 102, 103, 104, 105b	Upper member, Koobi Fora Formation	*Elephas recki* stage 3 *Mesochoerus limnetes* (progressive) *Metridiochoerus andrewsi* (typical) *Hippopotamus* sp. nov. (typical) *Ceratotherium simum* (progressive) *Tragelaphus* cf. *grandis*
Mesochoerus limnetes zone	105a, 130, 123	Lower member, Koobi Fora Formation	*Elephas recki* stage 2 *Notochoerus euilus* (progressive) *Mesochoerus limnetes* (typical) *Hippopotamus* sp. nov. (early) *Ceratotherium simum* (early) *Tragelaphus nakuae*
Notochoerus capensis zone	201, 202, 203	Kubi Algi beds	*Elephas ekorensis* *Notochoerus capensis* *Nyanzachoerus* sp. *Hippopotamus* sp. nov. (very early)

Vertebrate fossil zones of East Lake Rudolf.
From Maglio (1972): 382.

according to Leakey (1976b:482) might represent a separate species of *Australopithecus*. There is little evidence for the occurence of the gracile form of *Australopithecus* at East Rudolf except perhaps for a single cranium, KNM-ER 1813, from area 123 in the Lower Member from Koobi Fora Ridge S. West.

Members of the genus *Homo* are equally spread both geographically and spatially throughout the Koobi Fora Formation and Ilerat Member. These specimens according to R. Leakey and others show distinct morphological features that contrast markedly with the *Australopithecus* material from the same localities. Table II- 1 shows a partial list of the East Rudolf material attributable to the genus *Homo*. R. Leakey (1976b:481) claims that specimens of *Homo* from the Lower Member can be grouped into two types based on size. He is cautious in claiming that the two groups actually represent different species and states that further studies on the range of variability will allow for a final determination on the two *Homo* model. The best evidences for the smaller *Homo* form are KNM-ER 1501 and 1503, small mandibles with correspondingly small dentition. There is no known cranial evidence. The larger form of *Homo* is indicated by cranial remains, KNM-ER 1470 and 1590, and by a mandible, KNM-ER 1802, which in its known morphology resembles *Homo habilis* (OH 7,16) from Olduvai Gorge. The 1974-75 Expedition to East Rudolf discovered an additional 28 fossil hominid specimens. The most important finds consist of a well preserved partial innominate KNM-ER 3228 (area 102) and a relatively complete cranium KNM-ER 3733 (area 104) which according to Leakey (1976b) support the early prescence of *Homo* during the Plio-Pleistocene. Further evidence of the robust form of Australopithecina was witnessed in the mandible with complete dentition lacking only the ascending rami (KNM-ER 3230) which was discovered lying (15cm) above the main artifact-bearing horizon of site FxJj (Upper Member), and a left femur KNM-ER 3728 discovered _in situ_ in Area 100.

Table II-1

Specimens attributable to the genus *Homo* at East Rudolf

		Area		Area
KNM-ER #	164	104	1510	119
	730	103	1590	12
	731	6A	1591	12
	737	103	1593	12
	803	8	1800	130
	805	1	1801	131
	806	8	1802	131
	807 A-B	8 A	1803	131
	808	8	1804	104
	809	8	1805	130
	811	104	1806	130
	813	104	1807	103
	817	124	1808	103
	820	1	1809	121
	992	1	1810	123
	1462	130	1811	123
	1466	6	1812	123
	1470	131	1813	123
	1472	131	1814	127
	1475	131	1815	1
	1480	105	1816	6A
	1481	131	1817	1
	1483	131	1818	6A
	1501	123	1819	3
	1502	123	1820	103
	1507	127	3228	10
	1508	127	3733	104

Table II- 2

Specimens attributable to the genus Australopithecus at East Rudolf

		Area			Area
KMN-ER #	430	103	#	997	104
	404	7A		1171	6A
	405	105		1463	1A
	406	10		1464	6
	417	129		1465	11
	725	1		1467	3
	726	11		1468	11
	727	6A		1469	131
	728	1		1471	131
	729	8		1476	105
	732	10		1477	105
	733	8		1478	105
	736	103		1479	105
	738	105		1500	130
	739	1		1503	123
	740	1		1504	123
	741	1		1505	123
	801	6A		1506	121
	802	6A		1509	119
	805 A.B	1		1592	12
	810	104			
	812	104			
	814	104			
	815	10			
	818	6A			
	819	1			
	993	1			

EAST LAKE RUDOLF

Fossil Inventory

Found	Area	Number KNM-Er	Description	Published
1968	103	403	R. mandible corpus	Leakey, Mungai, Walker, 1971
1968	105	405	Maxilla edentulous	"
1968	7A	404	R. mandible corpus M $\overline{2-3}$	"
1968	129	417	Fragment parietal	"
1969	10	406	Cranium, edentulous	"
1969	10	407	Cranium, lacking face and maxilla	Leakey, 1971
1969	104	164a	Fragment parietal	"
1970	1	725	L. mandible corpus, edentulous	Leakey, Mungai, Walker, 1972
1970	11	726	L. mandible corpus edentulous	"
1970	6A	727	R. mandible corpus, edentulous	"
1970	1	727	R. mandible corpus, edentulous	"
1970	8	729	Mandible with dentition	"
1970	10	732	R. cranium, maxilla, frontal parietal	"
1970	103	730	L. mandible corpus, M_1-M_3, symp to RP_4	Leakey, 1971
1970	6A	731	L. fragment mandible corpus	"
1970	8	733	Cranial fragments, maxilla fragment, L. mandible	"
1970	103	734	Fragment parietal	"
1970	103	736	L. femur, shaft	Leakey, Mungai, Walker, 1972
1970	105	738	L. femur, proximal end and shaft	"
1970	1	739	R. humerus, distal end and shaft	"
1970	1	740	L. humerus, fragment of distal end	"

Found	Area	Number KNM-ER	Description	Published
1970	1	741	L. tibia, proximal end and shaft	Leakey, Mungai, Walker, 1972
1970	103	737	L. femoral shaft	Leakey, 1971
1971	104	164b-c	Additional two vertebrae, 2 phalanges	Day, Leakey, 1974
1971	8	803	Partial skeleton, postcrania, teeth	"
1971	6A	999	L. femur lacking lateral condyle	"
1971	6A	801	R. mandibular corpus M_2-M_3	Leakey, 1972
1971	6A	802	Isolated adult teeth	"
1971	1	805	L. mandibular corpus	"
1971	104	810	L. mandibular corpus -M_3	"
1971	104	812	Immature L. mandibular corpus	"
1971	104	814	Cranial fragments, frontal parietal	"
1971	10	815	L. femur without head	"
1971	104	816	L. upper canine	"
1971	6A	818	L. mandibular corpus P_4-M_3	"
1971	1	819	L. mandibular corpus	"
1971	1	993	R. femur	"
1971	104	997	Proximal metatarsal	"
1971	104	998	Lateral incisor	"
1971	6A	1170	Skull fragments	"
1971	6A	1171	Isolated juvenile teeth	"
1971	8	806	Isolated teeth A-F	"
1971	8A	807A	Fragment L. maxilla	"
1971	8	808	Isolated upper teeth A-G	"
1971	8	809	Fragments teeth	"
1971	104	811	Fragment parietal	"
1971	104	813	R. talus, fragment tibia	"

Found	Area	Number KNM-ER	Description	Published
1971	124	817	L. mandibular corpus	Leakey, 1972
1971	1	820	Immature mandible	"
1971	1	992	Mandible and dentition excluding incisors	"
1972	130	1462	Crown of lower M_3	Leakey 1973a
1972	1A	1463	Right femur diaphysis	"
1972	6	1464	Right talus	"
1972	11	1465	Prox. left fragment femur	"
1972	1	1466	Parietal fragment	"
1972	3	1467	Isolated M_3	"
1972	11	1468	Right mandible	"
1972	131	1469	Left mandible, M_3	"
1972	131	1470	Cranium	Day, Leakey, Walker Wood, 1975
1972	131	1471	Proximal half right	Leakey 1973a
1972	123	1821	Parietal fragment	Leakey, 1976
1972	131	1472	Right femur	Day, Leakey, Walker Wood, 1975
1972	131	1475	Proximal right femur	"
1972	105	1476	Left talus, proximal tibia and and fragmentary shaft	Leakey, 1973a
1972	105	1477	Juvenile mandible with teeth	"
1972	105	1478	Cranial fragments	"
1972	105	1479	Fragments isolated molars	"
1972	105	1480	Isolated molar	"
1972	131	1481	Left femur, proximal and distal end of tibia and distal fibula	Day, Leakey, Walker, Wood 1975
1972	131	1483	L. mandible fragments, roots I_2-M_1	"

Found	Area	Number KNM-ER	Description	Published
1972	123	1502	R. mandible body M_1, roots M_2	Leakey, 1973a
1972	123	1503	Proximal right femur	"
1972	123	1504	Distal right humerus	"
1972	123	1505	Left proximal and shaft fragment of femur	"
1972	121	1506	Right mandible $M_{\overline{1}-2}$ isolated $P^{\underline{3}-\underline{4}}$	"
1972	127	1507	Juvenile mandibular body alveoli decid. canine	Leakey, 1973a
1972	127	1508	RM_1 or RM_2	"
1972	119	1509	P_4-M_3 isolated	"
1972	119	1510	Cranial fragments	"
1972	103	1515	Isolated incisor	Leakey, 1976a
1972	12	1590	Cranial fragments with juvenile dentition	Leakey, 1973a,1974
1972	12	1591	Humerus lacking head	"
1972	12	1592	Distal half femur	"
1972	12	1593	Cranial and mandibular fragments	"
1972	105	1648	Parietal fragment	Leakey, 1976a
1972	123	1686	Cranial fragment	"
1973	8A	807B	Right maxilla fragment M^1	"
1973	130	1800	Cranial fragments	Leakey, 1974
1973	131	1801	L. mandible, P_4,M_1,M_3	"
1973	131	1802	L. mandible P_4-M_2 and R. P_3-M_2	"
1973	131	1803	R. mandible fragment	"
1973	104	1804	R. maxilla, P^3-M^2	"
1973	130	1805	Cranium and mandible	"
1973	130	1806	Mandible	"
1973	103	1807	R. femur shaft	"

Found	Area	Number KNM-ER	Description	Published
1973	103	1808	Assoc. skeletal and cranial fragments	Leakey, 1974
1973	127	1809	R. femur shaft	"
1973	123	1810	Prox. left tibia	"
1973	123	1811	L. mandibular fragment	"
1973	123	1812	R. mandibular fragment, left I_1 and M_1	"
1973	123	1813	Cranium	"
1973	127	1814	Maxillary fragments	"
1973	1	1815	R. talus	"
1973	6A	1816	Immature fragments of mandible	"
1973	1	1817	R. mandible	"
1973	6A	1818	Upper I^1	"
1973	3	1819	M_3	"
1973	103	1820	L. mandible with M_1	"
1974-75	6	2592	Parietal fragment	Leakey, 1976
1974-75	6	2593	Molar fragment	"
1974-75	6A	2594	Proximal fragment of tibia and fragment of tibia shaft	"
1974-75	1A	2595	Cranial fragments	"
1974-75	15	2596	Distal fragment of tibia	"
1974-75	15	2597	Molar crown	"
1974-75	15	2598	Occipital fragment	"
1974-75	15	2599	Fragment of premolar crown	"
1974-75	130	2600	Partial molar crown	"
1974-75	130	2601	Molar	"
1974-75	117	2602	Cranial fragments	"

Found	Area	Number KNM-ER	Description	Published
1974-75	117	2603-6	Tooth fragments	Leakey, 1976
1974-75	105	2607	Tooth fragment	"
1974-75	10	3228	Right innominate	"
1974-75	103	3227	Mandible with both $P_{\bar{3}}$ crowns	"
1974-75	131	3230	Mandible with full dentition	"
1974-75	100	3728	Shaft and neck of right femur	"
1974-75	102	3729	Body of left mandible, partil roots C-$M_{\bar{3}}$	"
1974-75	102	3730	Weathered distal femur	"
1974-75	105	3731	Body of left mandible partial roots I-$M_{\bar{3}}$	"
1974-75	105	3732	Partial cranium	"
1974-75	104	3733	Cranium	"
1974-75	105	3734	Body of left mandible C-M_2 fragment of $M_{\bar{3}}$	"
1974-75	116	3735	Weathered distal right humerus	"
1974-75	105	3736	Proximal 2/3 or radius	"

EAST RUDOLF

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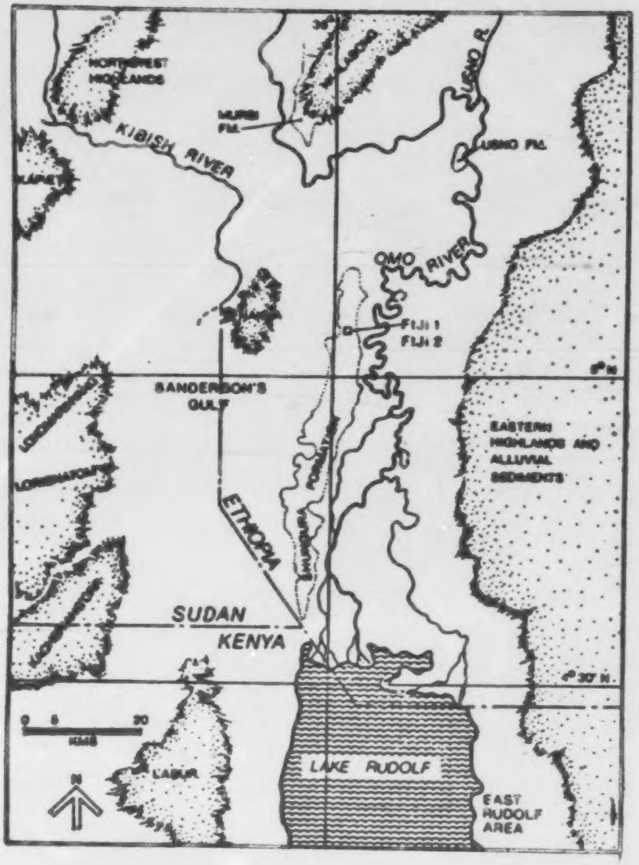
Figure II-25

THE LOWER OMO BASIN


NORTHWEST HIGHLANDS
36°
MURSI FM.
KIBISH RIVER
USNO R.
USNO FM.
OMO RIVER
FIJI 1
FIJI 2
5° N
SANDERSON'S GULF
EASTERN HIGHLANDS AND ALLUVIAL SEDIMENTS
ETHIOPIA
SUDAN
KENYA
4° 30' N
0 5 20
KMS
N
LABUR
LAKE RUDOLF
EAST RUDOLF AREA

(From Merrick et. al. (1973):572)

NORTH LAKE RUDOLF

LOWER OMO BASIN

GEOCHRONOLOGY

Southward from the Ethiopian highlands the Omo River empties into the northern end of Lake Rudolf producing an extensive delta. Beginning during the 1930's these exposures of Plio-Pleistocene age have been extensively explored by the late C. Arambourg, and joined more recently by Yves Coppens, Jan de Heinzelin and F. Clark Howell. From radiometric determination on lavas and interbedded tuffs, the Omo succession spans a range of time from more than 4 m.y. to less than 2 m.y.

The oldest sediments exposed in the Lower Omo Basin are those of the Mursi Formation which outcrop at the Yellow Sands locality near the southwestern edge of the Nkalabong highlands. This formation comprises three sedimentary members (I-III) composed primarily of clays, silts and sands with an aggregate thickness of over 140 meters and a terminal basalt member (IV). The sediments in members I and II are primarily deltaic with some evidence of fluvio-littoral conditions in the upper deposits. Radiometric determinations of the basalt of member IV yield a mean age of 4.2 m.y. The fossil fauna, especially the Suidae and Proboscidea, closely resemble those of Kanapoi.

The Nkalabong Formation unconformably overlies basalt member IV of the Mursi Formation. Its total thickness is nearly 90 meters and it has been lithologically divided into three members. The succession represents fluviatile deposits followed by wind deposited volcanic ash after which a series of littoral and tuff deposits were accumulated. Lacustrine deposits are common in the uppermost member of the Formation. No fossiliferous localities have been discovered however, two K-Ar determinations on feldspars from the Lapilli tuff (top of member II) have yielded an age of 3.95 m.y.

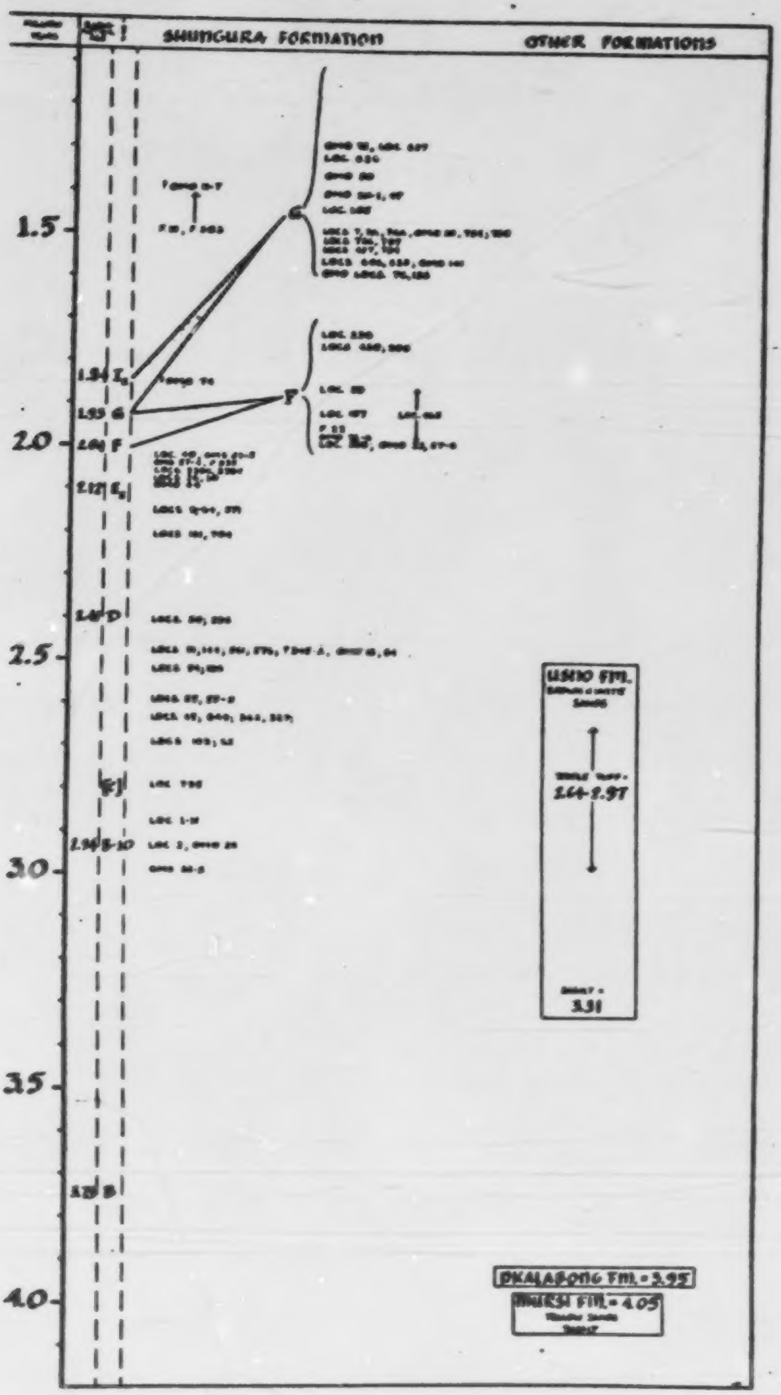
In the northeastern corner of the basin outcrops of sediments and lavas of the Usno Formation have a total aggregate thickness of about 200 meters. The sequence has been subdivided into nine members(A-I) which appear to represent fluviatile deposits, the result of floodplain and swamp situations. Two localities, designated White Sands and Brown sands, have yielded some 20 hominid teeth among an extensive vertebrate fauna. Radiometric determinations on the basal lava sequence (B) yielded an age of 3.3 m.y. From member G, the triple tuff sequence, an age of 2.6 m.y. was also determined. This age is equivalent to member C of the more southern Shungura Formation exposures.

The Shungura Formation (=Omo Beds) are the principal exposures between the Nakua volcanic hills and the lower reaches of the Omo River. The overall thickness of this formation is about 600 meters and represents a series of fluvial deltaic and lacustrine sands, silts and clays with intercollated tuffs. Ten prominent tuffs (designated A through J upwards) form marker horizons within the succession. A series of radiometric dates have been determined which span from 3.3 m.y. to 1.84 m.y. (member H). The stratigraphy of the sedimentary deposits have been investigated by Brown and Lajoie (1970), and consist of a basal member underlying a cyclic lithologic sequence of silts overlain by coarse to fine sands and silts and clays of members A through J, the result of rhythmic fluviatile deposition. Member H is the uppermost deposit in the series and is comprised of a fine pumicegravel. The Kalam West exposures, south of the Nakua volcanic hills, have recently been tied into the main Shungura succession and represent deposits younger than member J. Three additional members, K. L and M, are recognized above Tuff J and its overlying sediments. Tuff L has a radiometric age of 1.3 m.y. After deposition, the Shungura Formation, like the Usno Formation, was extensively faulted and both formations are unconformably overlain by upper Pleistocene/Holocene Kibish

Formation. Comparable deposits overlie the Koobi Fora succession in the East Rudolf area.

Localities yielding artifacts are not common in the main Omo deposits and absent from the Mursi and Usno succession. One locality (within member E of the Shungura Formation) has yielded a few artifacts and fragmentary bone. Other sparse occurrences (no occupation surfaces) have been recorded in sediments and tuffs of members G, D and C.

FIGURE 11-26



Stratigraphic relationship of hominid bearing localities of the Shungura and other formations of the Omo Succession, Ethiopia.
(From Howell and Coppens (1974):4)

274

Omo

Hominid Biostratigraphy

reference: F.C. Howell and Y. Coppens 1976

The following summary represents the latest analysis of the status of the fossil hominids recovered from deposits of the Omo succession, the Shungura and Usno Formations. Figure II-27 shows the chronostratigraphical relationships of the hominid specimens in the Omo succession.

Member B

Four specimens from Unit B-10 and 1 from Unit B-11 resemble the Usno homologues and cannot be distinguished on the basis of size, proportions and crown morphology from *A. africanus* from Sterkfontein, Makapans. Previously Howell (1969) and Coppens (1970) had suggested the prescence of two hominid taxa in upper member B, a view now considered in error.

Member C

18 localities in this member have yielded hominid remains, consisting mostly of isolated teeth (~30). A notable size increase appears in the hominid specimens from those of the Usno Formation. Though in morphology all closely approximate the *A. africanus* condition. The mandible originally referred by Arambourg and Coppens (1967) to *Paraustralopithecus aethiopicus* is distinguished by its low and robust body, markedly V-shaped internal mandibular contour; low, thick symphysis and dimensions and proportions which contrast with robust australopithecines. It is most comparable with homologues

from Sterkfontein of *A. africanus*. There is no convincing evidence for the prescence of more than one hominid species in Member C

Member D

(2.6 - 2.2) Hominid remains are known from 10 localities in this extensively channeled member. Except for a proximal humerus all specimens are isolated teeth. Though overall taxonomic affinity of the hominid samples is extremely difficult the deciduous dentition, the upper dentition, as well as the proximal humerus show important resemblances to *A. africanus*.

Member E

(2.12) Remains of hominids are known from 12 localities consisting of permanent teeth and a mandible fragment from the lowest units (E-3); and teeth, partial mandible and a complete ulna from the upper units (E-4,5). The lowest unit hominids are all comparable to *A*. africanus. However a number of specimens from E-3 suggest the prescence of a robust australopithecine, *A. bosei*. The juvenile partial cranium has an estimated cranial capacity of 420 cc and certain feature of the endocranial cast approach the *A. africanus* condition. The form and proportion of the occipital squama and planum are distinctive and seemingly unlike the condition, although not well known, in the gracil australopithecines. The dental specimens from the upper levels are not useful for taxonomic purposed. The partial mandible (Omo 57-4 locality) is very robust in body and symphysis with narrow intercanine distance for the incisors, a molarized P_4 and extremely large and broad molars an overall morphological pattern suggestive of *A. bosei*. The morphological features and size fo the right ulna (L40, Unit E-5) make it reasonable to assign it as well to *A. bosei*.

Member F.

Remains of hominids are known from 16 localities in this member. Only 2 hominid lower premolars and an upper molar come from the uppermost units, and all fall within the *A. africanus* known range of variation. In the lowest units of this member a more substantial sample is represented by 27 isolated teeth from two localities each related to Tuff F^1 and a mandible with partial dentition from an additional locality. Two associated lower molars from Location F-22, Kalam area clearly represent a robust australopithecine. Two other localities also yielded specimens similar to this taxon.

The remaining dentition and mandible with partial dentition represents theother australopithecine taxon similar to *A. africanus*. The evidence from member F suggests the prescence of two hominids though the dental morphology of the robust australopithecine is poorly known.

Member G

Hominid remains have been recovered from twenty-five localities and all but one locality is found within the prelacustrine fluviatile sedimentary units of the lower half of the member. These sediments have been dated to about 1.85 - 1.95 m.y. in age. Hominid remains consist of a series of teeth, three mandibles ranging from juvenile age to adulthood and a femoral shaft.

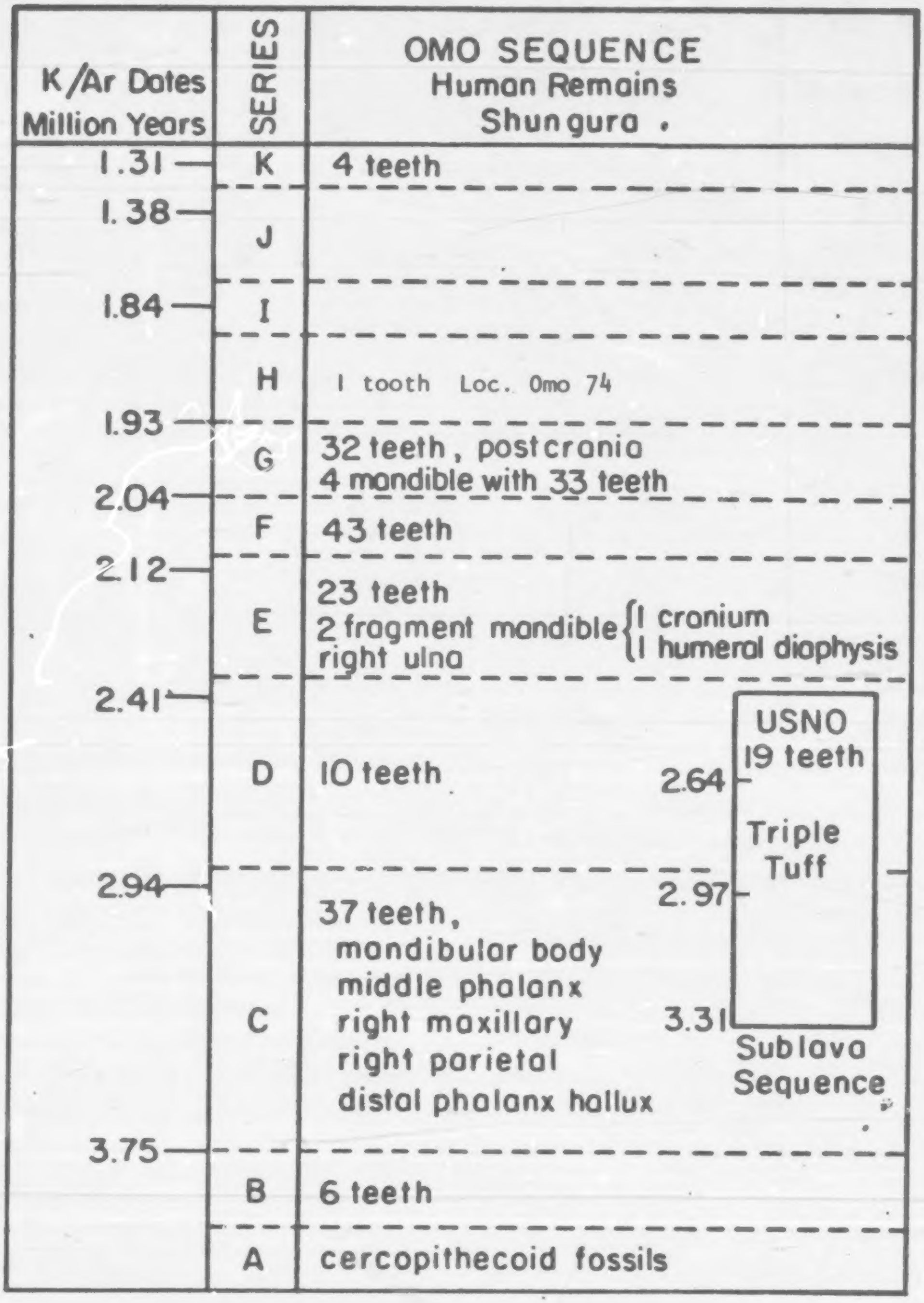
Hominids from the oldest localities (G-1,G-13, G-4) as well as more recent localities (G-718, G-12, G-13) from the lower half of the member approach the condition seen in both the robust and gracile forms of australopithecine. In G-5 however, the infant hemimandible from Omo locality 222 approaches the condition characteristic of *A. africanus* as well as *Homo*.

Additional isolated teeth are comparable to those specimens (OH 7, OH 13) assigned to Homo habilis. The upper half of the member consists of the postlacustrine sequence and represents the initial part of the Olduval Normal Event. The single hominid recovery of cranium and upper postcanine dentition suggest affinities with an early species of Homo. Member H. only a single locality (Omo 74) has yielded hominid remains consisting of a single tooth and incomplete metatarsal 3. The single tooth is an exact duplicate of that in the mandible of OH 13. Member K. a worn M_3 of indeterminate affinities as well as the fronto-parietal and orbito-temporal region of a cranium are known so far. The extreme thickness of the bones suggests the prescence of H. erectus in the upper sediments of this member representing the last portion of the Matuyama Revised Epoch.

Member L.

Two isolated teeth, an I^2 and a lower molar, have been recovered from two different localities. The lower molar is suggestive of Homo and is similar to OH 13.

Figure 11-27



K/Ar Dates Million Years	SERIES	OMO SEQUENCE Human Remains Shungura .	
1.31	K	4 teeth	
1.38	J		
1.84	I		
	H	I tooth Loc. Omo 74	
1.93	G	32 teeth, postcrania 4 mandible with 33 teeth	
2.04	F	43 teeth	
2.12	E	23 teeth 2 fragment mandible { I cranium I humeral diaphysis right ulna	
2.41	D	10 teeth	USNO 19 teeth 2.64
2.94	C	37 teeth, mandibular body middle phalanx right maxillary right parietal distal phalanx hallux	Triple Tuff 2.97 3.31 Sublava Sequence
3.75	B	6 teeth	
	A	cercopithecoid fossils	

OMO

Fossil Inventory
(AJPA (1974) 40(1))

Locality	Number	Description
Usno Fm. Brown Sands	B8-27	right I^1
	B8-23a	left P^4
	B8-14a	left P^4
	B8-14b	left P^4
	B8-4q	left P^4
	B8-23b	left m^1
	B7-39a	left P^3
	B7-39b	left P^4
	B7-36c	inc. m^1
	B-20	inc. dm^2
	B-28	inc. dm_2
White Sands	W-23	left P_4
	W-508	right m_1
	W-749	right m^2
	W-752	right m_1
	W-578	inc. left m_1
	W-750	frag. P^3
	W-751	inc. P_4
	W-753	right dm^2
Shungura Fm. Member B Loc 2	2-79	inc. $m_{2/3}$
	2-89	left m_3
Loc 1 North	1-292	frag. P.
	1-294	right m_3

Locality	Number	Description
Shungura Fm. Member B		
Loc Omo 28	28-19 (1967)	frag. right m_3
Loc Omo 28-S	28-30 (1968)	right m_3
Member C		
Loc Omo 18	18-18 (1967)	corpus mandible
	18-31 (1968)	left P^3
	18-32 (1968)	right m^1
	18-33 (1968)	left P_3
	18-34 (1968)	left $m_{1 \text{ or } 2}$
	18-35 (1968)	frag. $\underline{M}$
	18-36 (1968)	left I^1
	18-37 (1968)	right I^2
	18-38 (1968)	right I^2
	18-39 (1968)	right I^1
	18-40 (1968)	left I_1
	18-1799 (1970)	left m^1
	18-1848 (1970)	left middle phalanx, hand
Loc 45	45-2	right m_1
Loc 51	51-1	left m_1
	51-2	left m^1
	51-3	left m^2
	51-4	left m^1
	51-5	right I^1
	51-6	frag. right m^2
	51-7	inc. right $\bar{M}$
	51-79	right P_4
	51-80	right P_4

Locality	Number	Description
Shungura Fm.		
Member C		
Loc 54	54-20	inc. r. dm^2
Loc 55	55-33	right maxilla, roots $I^1 \rightarrow P^3$, P^4 crown
	55-34	frag. M
	55-57	left I^2
Loc 852	852-15	right I^1
Loc 849	849-1	frag. right m_3
Loc 62	62-17	right m_2
Loc Omo 84	84-100 (1970)	right m_3
Loc 136	136-9	frag. m_3
Loc 144	144-23	left dm^2
	144-24	inc. right dm_2
Loc 183	183-11	frag. M
Loc 327	327-16	I^2
Loc 345(A)	345(A)-11	subadult right parietal fragment
Loc 362	362-14	m_1
Loc 561	561-1	frag. left I^2
Loc 576	576-27	right dm_2
	576-18	right(?) distal phalanx hallux
Loc 795	795-1	right m_3
Member D		
Loc 9	9-11	inc. right m_3
	9-12	left m^3
	9-92	inc. left $m^{1/2}$
Loc 50	50-2	left m^3
Loc 64	64-2	left dm_2
	64-23	inc. dm_1 (?)
Loc 161	161-34i	frag. C (?)
Loc 296	296-1	right m_3

Locality	Number	Description
Shungura Fm.		
Member D		
Loc 571	571-2	left I^1
Loc 704	704-2	left dm_1
Member E		
Loc 10	10-21	inc. right m_3
Loc 26	26-1g	right m_2
	26-59	inc. left $m^{2/3}$
Loc 40	40-19	right ulna
Loc Omo 44	44-2466 (1970)	frag. mandible with roots of dentition
	44-1410 (1970)	right P^3
Loc Omo 57-4	57-41 (1968)	right hemi-mandible, frag. right P_4
	57-42 (1968)	inc. left m_1
	57-4.147 (1972)	frag. left m^3
	57-4.148 (1972)	frag. right P^3
Loc Omo 57-5	57-5.123 (1972)	frag. P.
	57-5.197 (1972)	frag. M.
	57-5.370 (1972)	frag. M.
	57-5.371 (1972)	frag. M.
	57-5.372 (1972)	frag. M.
Loc Omo 57-6	57-6.244 (1972)	inc. right m^2
Loc 338X	338X-32	frag. left dm^2
	338X-33	inc. P^3
	338X-34	left m^2
	338X-35	right P^4
	338X-39	left m_3
	338X-40	left P_4
	338X-41	right lower canine
	338X-42	frag. $\overline{M}$

Locality	Number	Description
Shungura Fm. Member E Loc 338Y	338Y-6	juvenile cranium, occipital with foramen magnum, left/right parietals
	338Y-9	juvenile humeral shaft
	338Y-89	frag. P^4
Loc P.933	P.933-1	left m^1
Member F Loc (Kalam) F.22	F.22-1a	right m_2
	F.22-1b	right m_3
Loc 28	28-28x	frag. left P_3
	28-30	right m_3
	28-31	right m_2
	28-58	right m^2
	28-125	right $\overline{C}$
	28-126	$\underline{P}$
Loc Omo 33	33-9 (1969)	right m_3
	33-10 (1969)	left m_2
	33-62 (1970)	right m^3
	33-63 (1970)	right $m^{1/2}$
	33-64 (1970)	frag. $\underline{m}$
	33-65 (1970)	left m_3
	33-506 (1971)	right P^3
	33-507 (1971)	left m^3
	33-508 (1971)	right P_4
	33-509 (1971)	left $\underline{m}$
Loc Omo 76	76-13 (1969)	frag. left m_3
	76-37 (1972)	frag. left m_3
	76-38 (1972)	frag. M/P
Loc Omo 76r	76r-11 (1969)	frag. right m_2

Locality	Number	Description
Shungura Fm. Member F		
Loc Omo 76r	76r-12 (1969)	frag. left $m_{1/}$.
Loc 157	157-35	left m_2
Loc 209	209-17	frag. $m_{1/2}$
	209-18	frag. $\underline{m}$
	209-30	frag. m
	209-31	frag. m
Loc 238	238-35	right m^2
Loc 398	398-14	frag. right m_1
	398-120	right P_3
	398-264	frag. right m_1
	398-265	frag. I
	398-266	frag. right m_3
	398-573	left m^3
	398-630	right m_3
	398-847	frag. right m_3
	398-1223	right P_4
	398-1215	frag. m
Loc 420	420-15	left P_4
Loc 465	465-111	frag. left P_4
	465-112	frag. left P_4
	465-113	frag. P
Member G		
Loc Omo SH-1	SH-1-17 (1969)	left m^1
Loc 7	7-279	left m_2
Loc 7A	7A-125	mandible with teeth excluding three incisors
Loc Omo 29	29-43 (1968)	right P_3

Locality	Number	Description
Shungura Fm. Member G		
Loc Omo 47	47-45 (1968)	left m_1
	47-46 (1968)	right m_2
	47-47 (1968)	frag. right m_3
	47-20 (1969)	frag. $\underline{m}$
Loc Omo 50	50-44 (1968)	right I^2
Loc 74A	74A-21	right hemimandible with $\overline{C}$ and P_4
Loc Omo 75	75-14a, b (1969)	associated upper and lower dentition with portion of right mandibular body left P_3, m_1-m_3; $P^4 \rightarrow m^2$ right $P_3 \rightarrow m_2$; $P^4 \rightarrow m^3$
Loc Omo 75i	75i-1255 (1970)	right P_3
Loc Omo 75-s	75-s-15 (1969)	left m_1
	75-s-16 (1969)	right m_3
	75-s-875 (1970)	right I_2 or $\overline{C}$
	75 s-1317 (1970)	proximal radius
Loc 105	105-7	lumbar vertebra
Loc Omo 136	136-72-1	left m_3
	136-72-2	inc. left m_3
	136-72-3	frag. right $\underline{m}$
Loc Omo 141	141-72-1	frag. left m^3 (?)
	141-72-2	frag. left $m^{1/2}$
Loc 427	427-7	partial right hemimandible erupting P_3-P_4, roots of dm_2 and m_1, complete m_2
Loc 626	626-45	left I^1
Loc 628	628-1	left P^4
	628-2	inc. left m_3
	628-3	left m_3

Locality	Number	Description
Shungura Fm Member G Loc 628	628-4	left P_4
	628-5	left P^4
	628-6	right I^1
	628-7	frag. m
	628.8	inc. $\underline{m}$
	628.9	left m_2
	628.10	left m_1
	628-224	inc. left P^3
Loc 686	686-3	left I^2
Loc 726	726-11	inc. P^3
Loc 754	754-8	part femoral diaphysis
Loc 797	797-1	frag. left P_4
Loc 894	894-1	cranial fragments and RP^3-RM^3, LP^3, LM^1-LM^3
Member H Loc Omo 74	(Tuffs 12-14)	right P_4
Member L Loc (Kalam) F.203-1	F.203	right m_3
Loc Omo K-7	K-7-19 (1969)	left m_2
Loc (Kalam) F.18-3	F-18	left I^2

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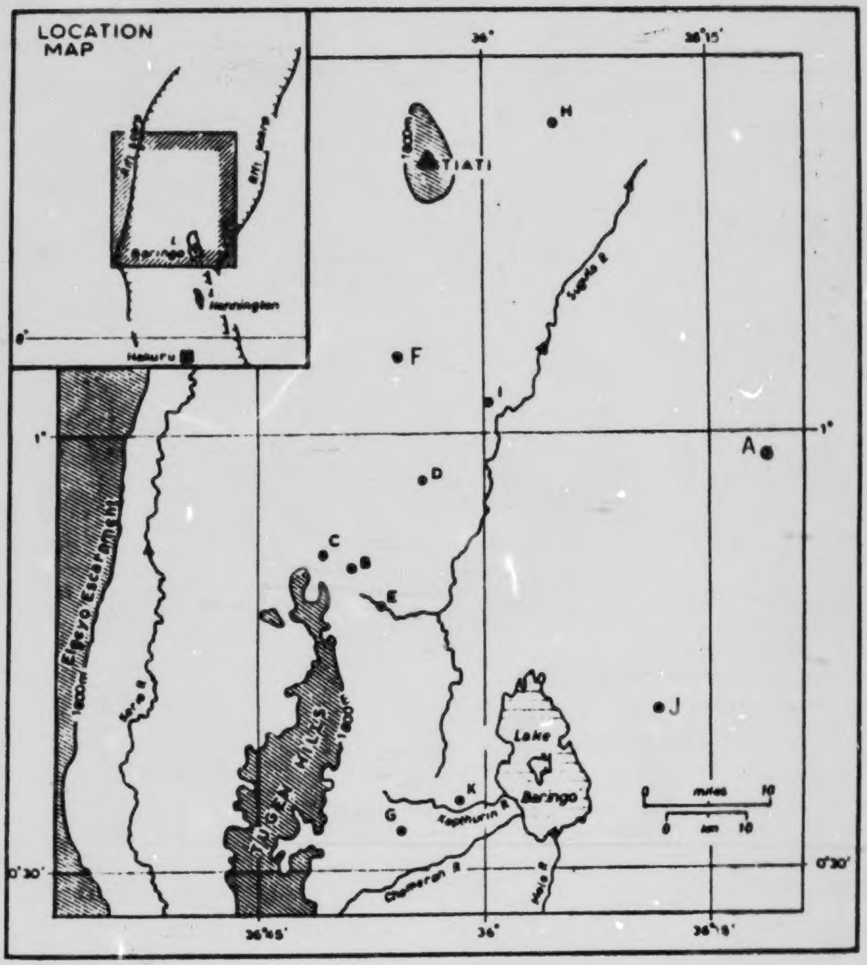
AREA IV

THE BARINGO BASIN
northern Kenya

Kapthurin Formation
Chemeron Formation
Aterir Beds
Lukeino Formation
Mpesida Beds
Ngorora Formation
Muruyur Beds
Chesowanja

FIGURE 11-28


LOCATION MAP
Baringo
0°
Nakuru
36°
36°15'
1800m
TIATI
H
Suguta R.
F
I
1°
A
D
C
B
E
Elgeyo Escarpment
1800m
Kerio R.
TUGEN HILLS
J
Lake
Baringo
miles
0
10
km
0
10
K
G
Kapthurin R.
Chemeron R.
0°30'
35°45'
36°
36°15'

Fossiliferous localities and sedimentary units in the Lake Baringo Basin. A- Alengerr Beds, B- Muruyur Beds, C- Ngorora Fm., D- Mpesida Beds, E- Lukeino Fm., F- Kaperyon Beds, G- Chemeron Fm., H- Aterir Beds, I- Karmosit Locality, J- Chesowanja, K- Kapthurin Fm.

(From Bishop, 1976: 150)

LAKE BARINGO

Fossiliferous sediments from localities in the west Baringo Basin are situated between the midline of the Gregory Rift which passes through Lake Baringo, and its western boundary fault at the Elgeyo escarpment falling into the Kerio Valley

Pliocene-Pleistocene sediments to the southwest of the Lake Baring area and east of the Kamasia (= Tugen) Hills were first recorded by Gregory in 1921 and later described as the Kamasia Lake Beds. These sediments actually represent two sedimentary sequences separated by a period of lava outpouring. The lower sequence has been named the Chemeron Formation, the upper sediments which rest unconformably on the lower ones, have been named the Kapthurin Formation. The area remained unmapped until 1960 when the Kenya Geological Survey made a preliminary reconnaissance. This initial mapping was followed by more detailed investigations of the East African Geological Research Unit of Bedford College, University of London. Preliminary descriptions of the sediments and fauna have been provided by Bishop and Chapman (1970) and Martyn (1967, 1969). The entire west Baringo sequence, as it is now known consists of sediments of the later Tertiary through Quaternary time divided into seven superimposed units occuring through 3000 meters of succession in the main scarp and foothills to the east of the Tugen Hills (Figure II- 28 this succession rests on Basement Complex rocks. The older part of the succession is exposed in the upper reaches of the main escarpment and is capped by the Kabarnet Trachyte lavas. The younger deposits are exposed between the base of the escarpment and Lake Baringo.

Three additional fossiliferous units outcrop further to the north: the Kaperyon Beds (F), the Aterir Beds (H) and the Karmosit Beds (I) (Figure II-

TABLE II-3

Stratigraphic Succession in the West Lake Baringo Basin
Reference: W.W. Bishop 1976.

Sedimentary Units	Volcanic Units	K/Ar ages
Kapthurin Formation	Loyamarok phonolite	1.0 -.23 m.y.
Chemeron Formation	Ndau mugearite interbedded near the top of the Chemeron sediments	2.0 - 2.1 m.y.
Aterir Beds overlies the Ribkwo volcanics		2.9 m.y.
	Ribkwo volcanics	
Karmosit Beds[1] (3.4 - 4.4 m.y.)		
Kaperyon Beds[1] (3.7 - 5.4 m.y.)	Kaparaina basalts underlies the Chemeron Fm. and overlies the Lukeino Fm.	4.4 - 5.1 m.y.
Lukeino Formation overlies the Kabarnet trachyte		6.7 m.y.
	Kabarnet trachyte	
Mpesida Beds interbedded with the Kabarnet trachyte		7.2 - 7.7 m.y.
	Sumet phonolite	7.95 - 9.75 m.y.
Ngorora Formation overlain by the Sumet phonolite		12.0 - 12.1 m.y.
Muruyur Beds interbedded between the Tiim phonolite	Tiim phonolite	13.15 - 14.3 m.y.

[1] The Karmosit and Kaperyon Beds are not directly within the West Baringo sequence, but are exposed in the northern region of the basin. See Figure II- 28.

THE CHEMERON FORMATION (G) is extensively faulted, has an aggregate thickness of some 250 meters, divided into five principal units. These units include (1) the Basal Beds, which have yielded a fossiliferous mammalian assemblage and are composed of fluviatile gravels and coarse angulated sands, (2) the Lower Fish Beds, represented by fluviolocustrine silts and superimposed lacustrine silts and shelly limestones separated from (4) the Upper Fish Beds by Layer (3), the Lower Tuffs. Layer (5) is a series of waterlaid, stratified tuffs.

The sedimentary sequences are overlain by fine-grained lavas yielding K-Ar ages between 1.5-2.0 m.y. Faunal analysis of several localities within the Basal Beds, however, show similarites to assemblages from Kanapoi and the Mursi Formation of the lower Omo Basin indicating much older ages, nearer to 4.0 m.y.

The only remains of Hominidae know from the Chemeron Fm. consist of an isolated temporal bone from locality JM 85 in the Upper Fish Beds. The bone includes the mandibular fossa, the tympanic and external auditory meatus, part of the mastoid, the root of the zygoma and most of the petrosal. The bone has been described by Tobias (1967), who suggested that most of the features of the temporal resemble those of known species of australopithecine.

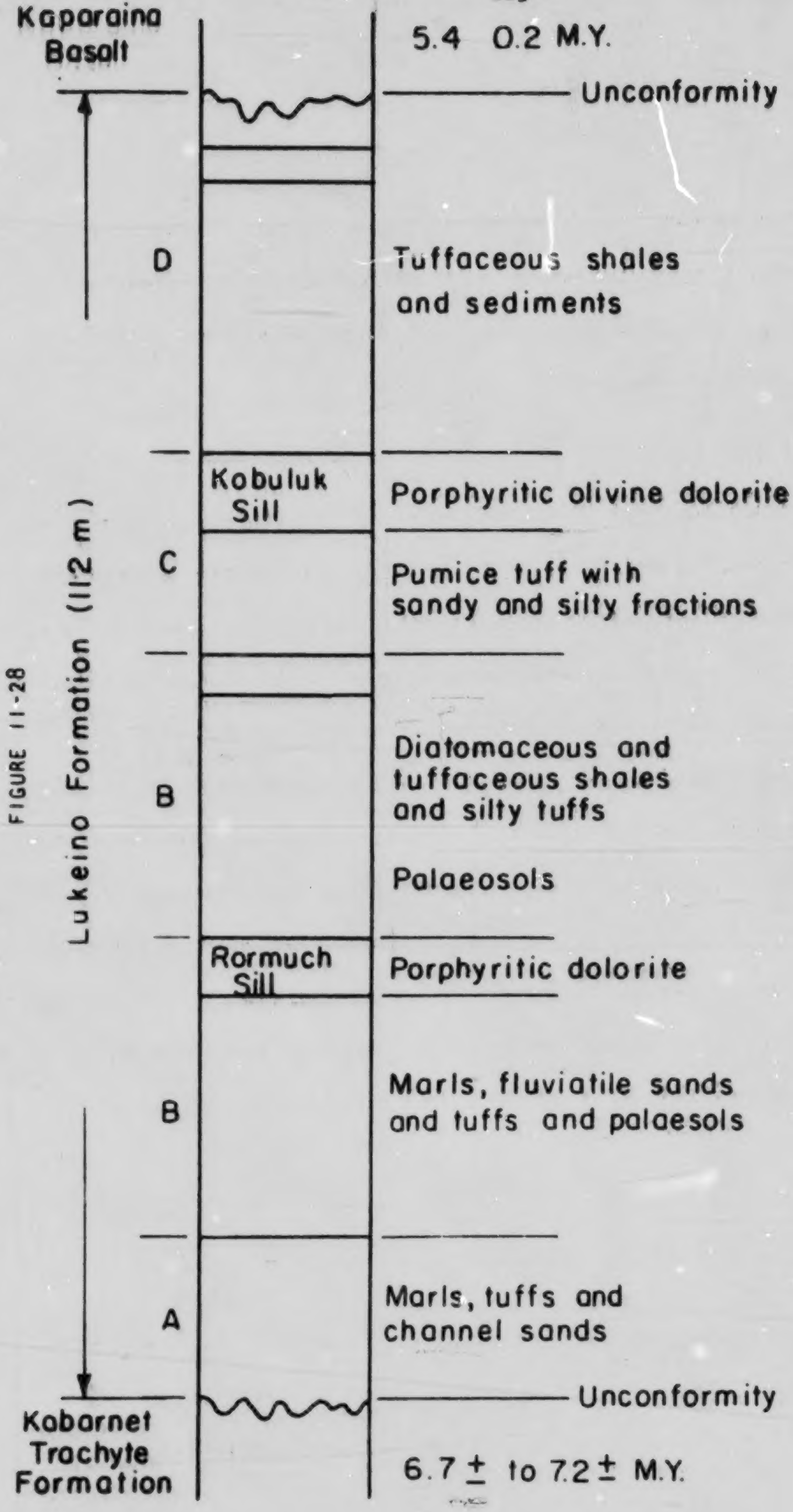
Lying below outcrops of the Chemeron and underlying Kaparaina Basalt is a recently described series of deposits named the Lukeino Formation and described by Pickford (1975). Mapped during 1973 as part of the investigations of Bedford College, London, these exposures extend our knowledge of sediments and associated vertebrate assemblages back to 6.5 m.y.

THE LUKEINO FORMATION (E) is composed of about 130 meters of primary and reworked volcanic rock, and basin deposited sediments. Though it is exposed over an area of 450 km^2, the outcrop is not continuous. Lying below these deposits is the Kabarnet Trachyte Formation which has yielded a K-Ar date of 6.7-7.0 m.y. The sedimentary group is composed of four recognized members A-D (earliest to latest) with three sills intruded into the members, two of which were embedded before the deposition of Member D. The third sill (the Cheseton Sill) is not represented in the type section shown in Figure II Relative uplift after the deposition of Member D resulted in erosion of the formation to the basal member. The eroding exposures were then capped by basalts of the Kaparaina volcanics, for which the mimimum age has been radiometrically determined at 5.4 m.y.

A list of fauna collected from the Lukeino Formation from forty-seven localities is provided. (page 283). Most of the fossils were recovered from Members A and B. Hippopotamidae are abundant while the bovids, suids and giraffids are scarce. Paleoenvironmental reconstruction suggests prevalent lacustrine conditions during deposition. Fossil flora is also common in the form of leaves, grass, ferns and diatoms.

A single lower molar tooth represents, the only hominid specimen to be recovered from these deposits to date. Although a surface fine, the coloration of the tooth relates it to a fossiliferous horizon which lies in the middle of Member A at Locality 2/219 at Chepboit. KNM LU335 is a left lower, probably unerupted, molar similar in general dimensions to the M_2 of the chimpanzee. Morphologically it is similar to the robust forms of Australopithecus. The tooth is hominid-like by having two equally divided occlusal basins. This

FIGURE 11-28


Kaparaina Basalt
5.4 0.2 M.Y.
Unconformity
D
Tuffaceous shales and sediments
Lukeino Formation (112 m)
Kobuluk Sill
Porphyritic olivine dolorite
C
Pumice tuff with sandy and silty fractions
B
Diatomaceous and tuffaceous shales and silty tuffs
Palaeosols
Rormuch Sill
Porphyritic dolorite
B
Marls, fluviatile sands and tuffs and palaesols
A
Marls, tuffs and channel sands
Unconformity
Kabarnet Trachyte Formation
6.7 ± to 7.2 ± M.Y.

298

TYPE SECTION AT KOBULUK

(Redrawn from Pickford, 1975)

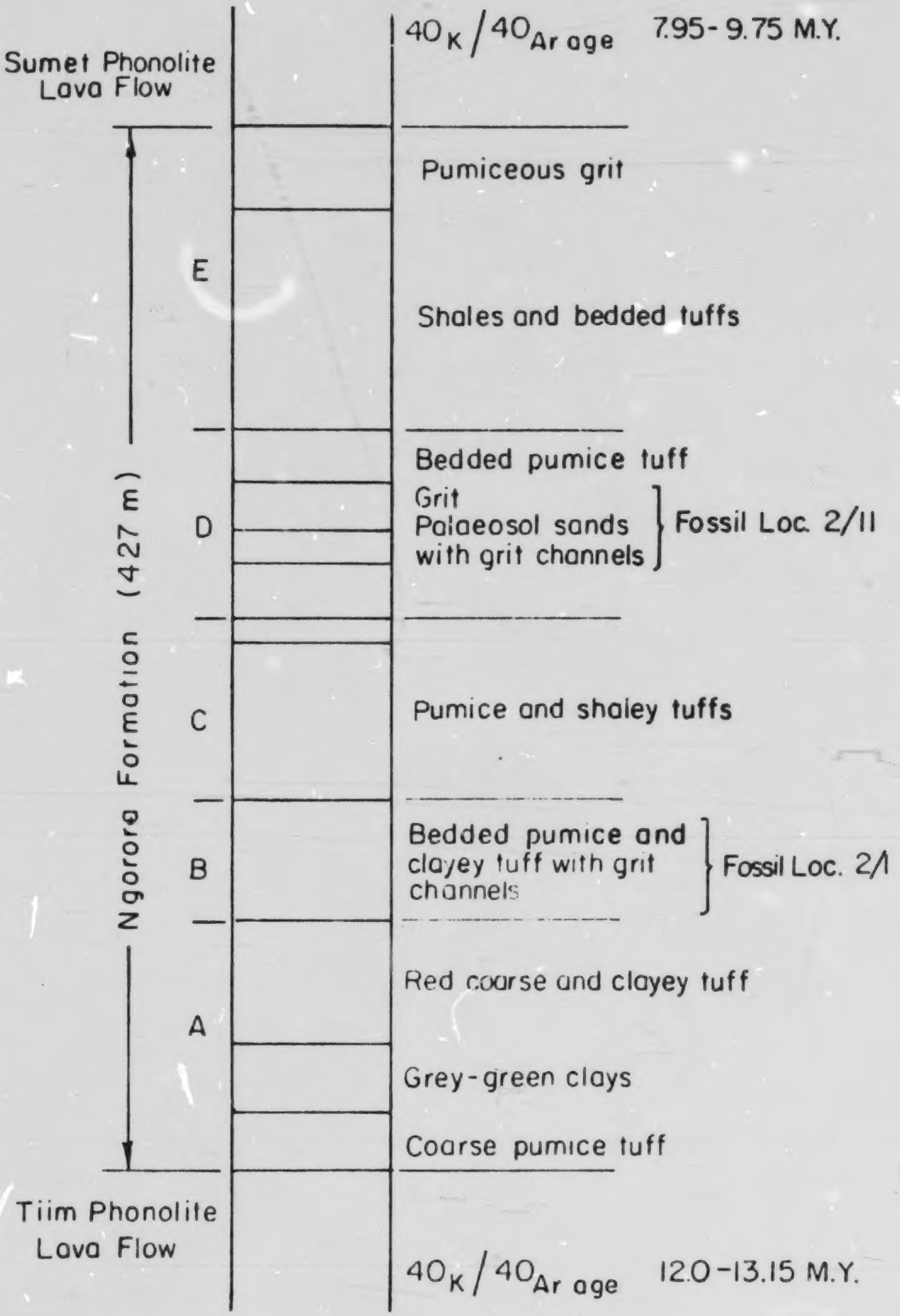
indicates that the protocone and hypocone of the upper molar were of equal size (as is the condition of the upper molar from the Ngorora Formation). It is quite different from the Dryopithecine Pattern which show a relatively smaller trigonid basin on the crown surface.

THE NGORORA FORMATION (C)

Older sedimentary outcrops which have yielded fossiliferous localities have been described by Bishop and Chapman (1970) on the western escarpment of the Kamasia Hills, twenty miles northwest of Lake Baringo. Investigated during 1968 and 1969, these fossiliferous sediments are underlain and overlain by lava flows yielding dates for the sediments between 9.0 and 12.0 m.y. The sedimentary layers consist of lithologically variable waterlaid deposits some 360 meters in thickness. Five lithological subdivisions have been described labeled A-E. The single fossil hominid discovered was described by L.S.B. Leakey in the article by Bishop and Chapman (1970) and consisted of an upper molar crown. Anterior and posterior wear facets are present suggesting that the tooth was an upper second molar. The crown was described as being very low relative to overall size and could be attributed to the genus Australopithecus.

EAST BARINGO SEQUENCE

Two sedimentary units have yielded mammalian fossils. The Alengerr Beds (A) are poorly exposed and the recovered mammalian fauna is restricted. The sediments occur within a sequence of Phonolites and are approximately 14.0 - 12.5 m.y.


$^{40}K/^{40}Ar$ age 7.95-9.75 M.Y.
Sumet Phonolite Lava Flow
Pumiceous grit
E
Shales and bedded tuffs
Bedded pumice tuff
D
Grit
Palaeosol sands with grit channels
Fossil Loc. 2/11
C
Pumice and shaley tuffs
B
Bedded pumice and clayey tuff with grit channels
Fossil Loc. 2/1
Ngorora Formation (427 m)
A
Red coarse and clayey tuff
Grey-green clays
Coarse pumice tuff
Tiim Phonolite Lava Flow
$^{40}K/^{40}Ar$ age 12.0-13.15 M.Y.

GEOLOGICAL COLUMN OF THE NGORORA FORMATION, LAKE BARINGO (Redrawn from Bishop and Chapman, 1970)

FIGURE 11-29

CHESOWANJA (J)

To the east of Lake Baringo, additional sedimentary series were discovered by J. Carney in 1970. These lacustrine deposits are contained in an embayment along the foot of the Aruru escarpment in the western part of the Chemoigut sedimentary basin. The basin itself was the result of Upper Pliocene-Pleistocene volcanics which formed barriers damning the drainage from the eroded region above the escarpment.

The fossiliferous sediments have produced a series of fauna and flora species yielding data of the environment of perhaps 1.1 to 1.2 m.y. One potassium-argon yields a date for a lava of 1.2 ± m.y. Seven of the fourteen identified mammalian genera have modern counterparts in Africa, and the total assemblage has elements in common with that from Olduvai Bed II and Peninj in Tanzania.

Hominid remains (KNM-CH1) consist of most of the right facial skeleton together with parts of the left facial skeleton, right frontal, and the right basal calvaria including the petrosal. Upper right maxillary dentition $C \longrightarrow M^{3}$ are intact. Affinities of the specimen are with *Australopithecus robustus* in the size and massiveness of the face, buccolingually expanded cheek teeth, and a broad dished face.

Endocranially, the specimen appears to have possessed much larger anterior and middle cranial fossae than is seen in Olduvai Hominid 5 or SK 1585, and much larger than in the available specimens of *A. africanus*. A rough estimate of the endocranial volume is given at more than 530 cc. The specimen is the youngest known representative of the large form of *Australopithecus* which shows, however, many features such as enlarged cranial capacity, face positioned more below the brow case, and reduction of the size of the temporalis muscle, suggesting morphological advances in the direction which lead to the genus *Homo* in other lineages.

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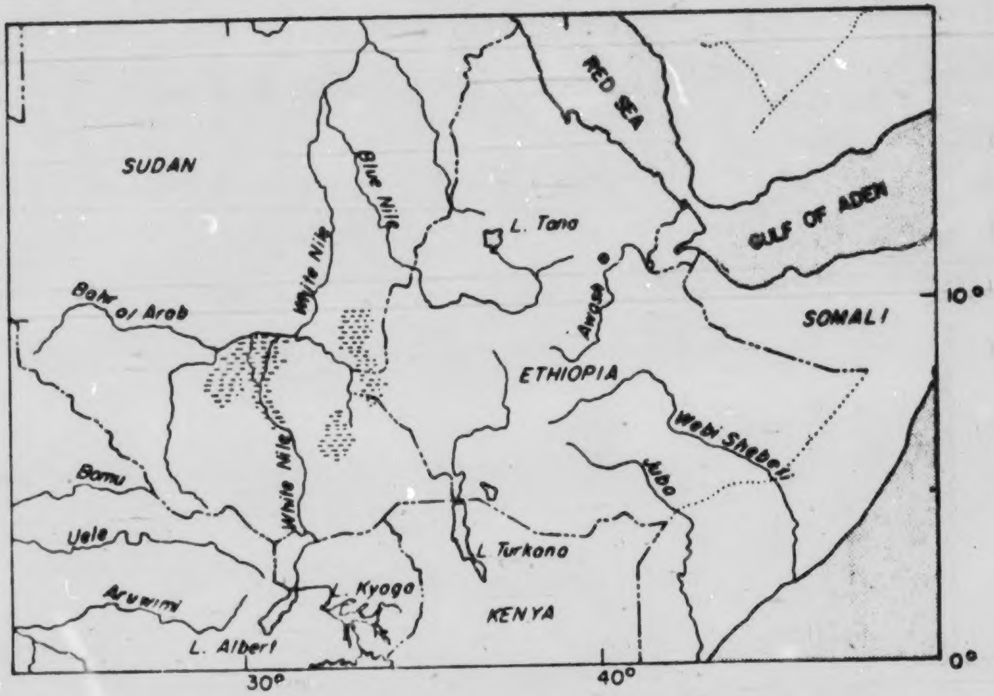
AREA V

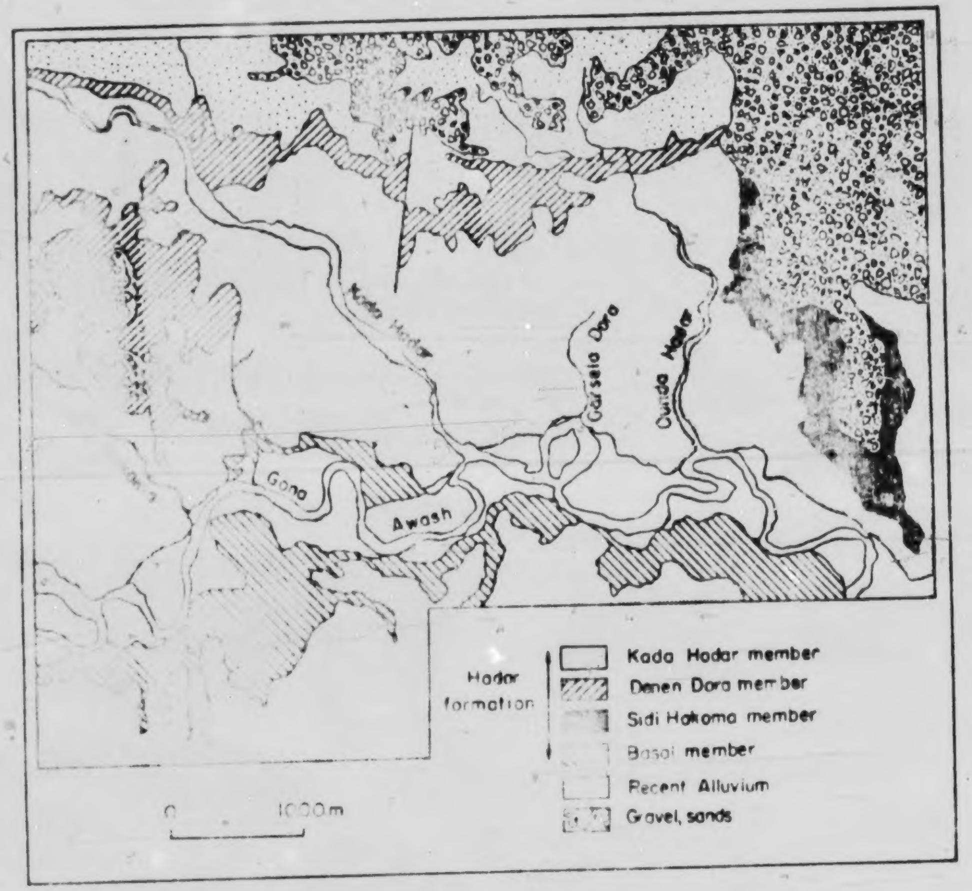
THE AFAR TRIANGLE
ETHIOPIA

Hadar, Awash River

FIGURE II- 30


SUDAN
Blue Nile
RED SEA
GULF OF ADEN
L. Tana
White Nile
Bahr el Arab
Awash
SOMALI
ETHIOPIA
Webi Shebeli
Juba
Bomu
Uele
White Nile
L. Turkana
Aruwimi
L. Kyoga
KENYA
L. Albert
30°
40°
10°
0°

THE AFAR TRIANGLE, ETHIOPIA (Hadar site)


Kada Hadar
Garsela Dora
Ouida Hadar
Gona
Awash
Hadar formation
Kada Hadar member
Denen Dora member
Sidi Hakoma member
Basal member
Recent Alluvium
Gravel, sands
0
1000m

Geological Map of northern Hadar

GEOLOGY AND DISCOVERIES OF THE AFAR TRIANGLE

The Afar Triangle or Afar Depression comprises parts of various Ethiopian Provinces including Erythrea, Tigrai, Wallo and Harrar, as well as the French Territory of the Afars and the Issas (T.F.A.I.). The Depression has been investigated by French geologists since 1967, although earlier explorations have been undertaken since 1814.

The entire region has been subdivided and described in two parts. The northern half of the Depression has been called the "Danakil" Depression and begins with a northern apex in the Gulf of Zula, Red Sea. The "Danakil" is bounded to the west by the Ethiopian highlands and the escarpment, and to the east by the Danakil Alps.

The southern continuum of the Afar Triangle includes the Central Afar Region and the T.F.A.I. The base of the triangle is demarcated by the Somali Plateau. Throughout the area, volcanic and sedimentary formations from Miocene through Quaternary in age are exposed and interbedded.

From earliest Miocene, volcanic activity has been continuous within the Depression. The volcanic unit referred to as the "stratoid series" is characterized by flood basalts and rhyolites (acidic lavas) and as a unit covers a time interval from at least 4 m.y. up to recent Quaternary.

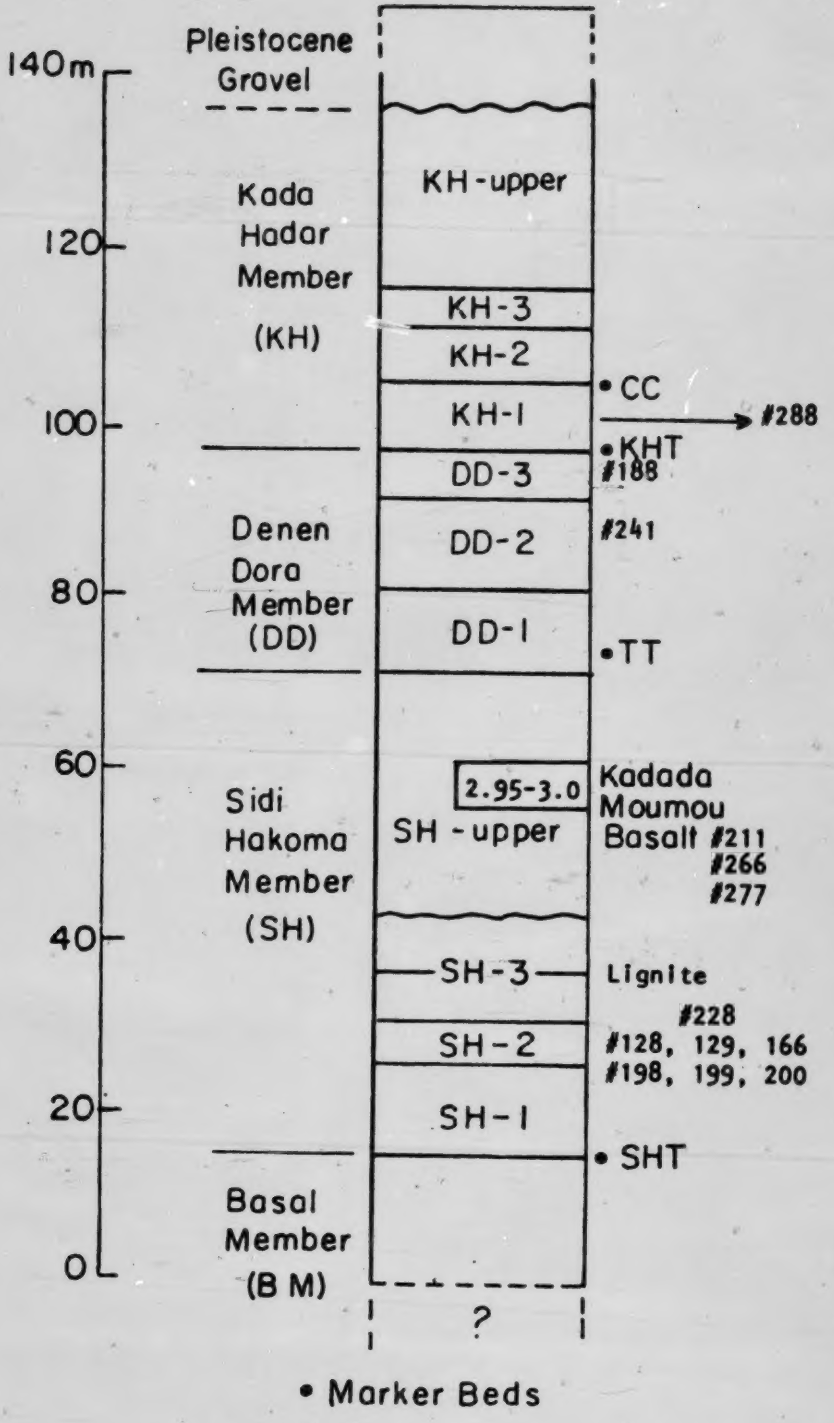
Aside from the Tendaho graben which contains Lake Abbe, the only sedimentary deposits of Plio-Pleistocene age are those in the west central plateau. The extent of this sedimentary basin referred to as the Central Afar Group is approximately 60 km wide by 150 km long. The basin is limited to the west by the Ethiopian escarpment and to the northeast by the Magenta Plateau. Much of the sedimentary sequence is capped unconformably by an uppermost unit of Pleistocene gravels and bedded sands which contain Achuelean artifacts.

Fossil hominid discoveries have been reported from the Central Afar Group in sediments exposed in the drainage of the Awash Basin in the tributaries of Gona, Sidi Hakoma, Kada Hadar, Ounda Hadar and south of the Awash River in a zone ranging between the parallels 11° and 40° 30' East are referred to as the Hadar site encompassing about 42 km^2.

The Awash-River flows from the South to the North along a longitude approximating 40° 30' East. The sediments thus exposed are referred to as the Hadar Formation even though the maximum extent of the deposits has not been worked out. THe sediments represent lacustrine, lake margin and associated fluvial deposits related to a Plio-Pleistocene lake. Most of the vertebrate fauna is found in the sand and sandstones of the sequence. The frequent occurence of relatively complete and associated fossil specimens and the lack of taphic abrasion indicated a low energy depositional environment coupled with a possibly high rate of sedimentation.

The formation has an exposed thickness of 120 - 140 m with no major time gaps suggested by the several minor erosional unconformities. The Hadar Formation has been subdivided into four members each consisting of three or more submembers and each separated by major tuff horizons. As indicated on the generalized geological cross section (Figure II- 31)from the base to the top, the members are labeled (1) the basal member (BM); (2) the Sidi Hakoma member (SH) defined from the former by a series of white tuffs (SHT) at its base; (3) the Denen Dora member (DD) with a series of thin tuffs (TT) contained within an extensive clayey marker horizon at its base; and (4) the Kada Hadar member (KH) separated from (3) by a single tuff (KHT). Data derived from separate sources suggest a short duration of sedimentaion for the formation, probably less than 1 m.y. with no major time gaps.

FIGURE II-31


140m
120
100
80
60
40
20
0
Pleistocene Gravel
Kada Hadar Member (KH)
Denen Dora Member (DD)
Sidi Hakoma Member (SH)
Basal Member (B M)
KH-upper
KH-3
KH-2
KH-1
DD-3
DD-2
DD-1
2.95-3.0
SH - upper
SH-3
SH-2
SH-1
?
• CC
#288
• KHT
#188
#241
• TT
Kadada Moumou Basalt #211
#266
#277
Lignite
#228
#128, 129, 166
#198, 199, 200
• SHT
• Marker Beds

GEOLOGICAL COLUMN OF THE HADAR FORMATION

At the eastern end of the Hadar site the Kadada Moumou subplateau contains a single basalt flow which overlies sedimentary deposits of clays and silts. Most of the sediments above the basalt are of the Post Hadar gravel unit, however in one locality sediments of the Hadar Formation are found to overlie the basalt. There is no fault between the Kadada Moumou flow and the Hadar sedimentary sequence and stratigraphically 20 meters above the flow is the persistent TT marker horizon of the Denen Dora member. The Kadada Moumou basalt, therefore, figures in the upper portion of the Sidi Hakoma member. K-Ar determinations of the basalt yield consistent results ranging from 2.95 to 3.0 ± 0.2 m.y.

Paleomagnetic determinations were taken from two sections sampled. The lower paleomagnetic sequence consists of the basal member upward to the SH-2 unit. The upper section spans KH-1,-2 and the lower part of KH-3. The Kadada Moumou basalt separating the two sections was also sampled. Both sedimentary sequences are magnetized normally whereas the basalt show reversed magnetization. The interpretation is that the reversal represents the Mammoth or Kaena events within the Gauss normal epoch.

The Hadar area has produced over 250 fossiliferous localities yielding over 6000 specimens of some 40 species of mammals. The fauna collection is broadly comparable to Omo I biostratigraphic unit. A provisional division into three faunal subunits has been proposed by B. Gray and would consist of a lower unit (SH-1 → SH-2), a middle unit (SH-3 → DD-2), and an upper unit (DD-3 → to top). Most of the taxa listed on Page 289 are represented in all three units although the proportions vary.

The Afar-Hadar area was first explored by a short reconnaissance expedition in 1972. The outcome of this expedition was the International Afar Research Expedition organized by Maurice Taieb of the Laboratory of Quaternary Geology, France, and co-directed by D. Carl Johanson of the Cleveland Museum of Natural History. The Hadar site was chosen for intensive study because of its presumed antiquity, excellence in preservation of fossil materials and clear, laterally continuous marker-horizons and volcanics.

The first discovery of fossil hominid remains in the Hadar region were made on October 30, 1973 when four associated lower limb fragments (AL 128, 129) were collected. From locality AL 129, a sandstone ravine, the first hominid specimen was recovered on the surface and consisted of a distal femur and a proximal tibia. The femur is notable for its marked angle of the shaft, yet the size is similar to that of a chimpanzee. At this same locality an additional right proximal femoral end was collected. This femoral fragment is missing the entire neck and head posteriorly and the anterior surfaces of the greater trochanter which are crushed. This damage appears to have been inflicted while the bone was fresh perhaps by the activity of a carnivore. (AJPA 45(2): 217). A fragment of a left proximal femur was also collected some 80 meters away (Locality 128) and consists of the shaft and both trochanters but lacks the head and most of the neck. Details of the anatomy suggest that the left femur belongs to the same individual as the right. The right distal femur as well as the right proximal tibia also appear to belong to this same individual. In December the only other hominid discovery was made some 500 meters (Locality 166) from these postcranial fragments, a fragment of a heavily eroded left temporal including the external ausitory meatus was found and anatomically resembles that of the robust form of Australopithecus. The long bones are more reminiscent of those of A. africanus.

Additional discoveries were made during the 1974 field season of approximately 10 individuals including an intact partial skeleton. The first two discoveries were one complete (AL 200-1) and one half maxilla (AL 199-1) recovered from the same mudstone as the original 1973 discoveries. The AL 200 specimen shows pronounced alveolar prognathism with large maxillary sinuses and guttered lower nasal margin. Both maxilla are similar in morphological features.

The remaining discoveries are labeled and described in the inventory of fossil hominids. Dental measurements are published in Johanson and Taieb (1976).

On November 24, 1974 a partial skeleton was discovered eroding from a sand deposit from a stratigraphic horizon above the KHT. Analyses of the skeletal material are in process. The remains are those of an alleged female gracile australopithecine at Afar Locality 288. The remains consist of nearly 40% of the skeleton representing the hand, wrist, right arm, leg, mandible and cranial fragments, and one-half of the pelvis with an articulating sacrum. Nicknamed "Lucy", the skeleton represents the most complete discovery of an early hominid from the Plio-Pleistocene period.

The pelvis appears to be that of a female with a broad sciatic notch, a pubis with a pronounced ventral arc and an obtuse subpubic angle. The ilium however seems to be higher and the anterior border straighter. The shoulder, elbow and hip joints are intact. The left femora is estimated to measure 270-280 mm and, compared to the humerus, estimated to be about 235 mm, is relatively short. The humeral-femoral index is 83.9 compared to that of about 73 for Homo sapiens and 100-135 for the living apes demonstrating that the forelimbs were somewhat longer compared to the hindlimbs than in modern hominoids. In size the specimen resembles Sterkfontein (STS 14).

The mandible is not heavily built, the teeth only slightly worn. The buccal surface of the lower P3's slope in the almost complete absence of a metaconid and resembles that of the sectorial shape in pongids. The form of the dental arch is V-shaped, the incisor region being quite reduced. The canine is relatively longer and possibly slightly projecting. The cranium is fragmentary; there appears, however, to have been no substantial development of the nuchal or temporal musculature.

AL 288 appears to be somewhat more primitive that STS 14 in the morphological features of the pelvis. The shallow acetabulum and relatively high ilium as well as the V-shaped mandible is noteworthy. Figure II-31 indicates the position of the Hadar localities in stratigraphic succession. The postcranial material discovered in 1973 situated 80 meters below has been considered similar to that of AL 288 and is probably of the same taxon.

The presence of another taxon is suggested by additional postcranial specimens AL 211-1, which resemble closely Olduvai Hominid #20 from locality HWK 11 assigned to _A_. _boisei_, and two proximal femora from Swartkrans (SK 82, 97) assigned to _A_. _robustus_. Features of the large australopithecine are also seen in the temporal fragment (AL 166-9) resembling material from Swartkrans and East Rudolf, particularly in the large bulbous mastoid process and broad temporal shelf.

A third hominid form has been reported based on a complete maxilla (AL 200-1a) and a right maxillary fragment (AL 199-1) discovered in stratigraphically equivalent localities. The complete maxilla has rather large canines, broad incisors and a large postcanine dentition reminiscent of P. IV from the Djetis Biozone of Java as well as KNM-ER 1590 assigned to the genus _Homo_ from East Rudolf. However, primitive characters are seen in the guttered nasal margin and alveolar prognathism. The mandibles AL 266-1 and 277-1 also resemble in morphological detail specimens assigned to _Homo_ such as OH #7 and KNM-ER 1802. Thus to date the Hadar hominids according to the workers in the field represent three different hominid taxa. Their results are still preliminary and further revision is expected.

Fossil Hominids of The Hadar Site

Found	Area	Number	Description
Oct.1973	128	128-1	Left proximal femur fragment
Oct.1973	129	129-1a	Right distal femur
Oct.1973	129	129-1b	Right proximal tibia
Oct.1973	129	129-1c	Right proximal femur fragment
Oct.1973	166	166-9	Left temporal fragment
1974	188	188-1	Right mandible M_2-M_3
1974	198	198-1	Left mandible C-P_4 dm, M_1-M_2
1974	198	198-17a,b	Left I^1 and I^2
1974	198	198-18	Right I_2
1974	199	199-1	Right maxilla, C-M^3
1974	200	200-1a,b	Complete maxilla with dentition, Right $M_{\bar{1}}$
1974	211	211-1	Right proximal femur fragment
1974	228	228-1	Diaphysis of right femur
1974	241	241-14	Left lower molar
1974	266	266-1	Mandibular corpus, left P_3-M_1, right P_3-M_3
1974	277	277-1	Left mandibular corpus, C-M_2

Al 288-1		fragment of diaphysis of femur
	A	(occipital fragment)
	B-H	(additional cranial fragments)
	I	mandible with right P3-M3 and left P4 and M3
	J-K	mandibular condyles
	L	glenoid cavity of the right scapula
	M	right humerus
	N	proximal part of right ulna
	O	distal part of right ulna
	P	proximal part of right radius
	Q	distal part of right radius
	R	proximal part of left humerus
	S	distal part of left humerus
	T	proximal part of left ulna
	U	distal part of left ulna
	V	distal part of left radius
	W	left os magum (capitate)
	X-Z	phalanges
	AA-Ab	lumbar vertebrae
	AC AM	dorsal vertebrae 6
	AI AM	vertebral fragments
	AN	Sacrum
	AO	left ilium
	AP	left femur
	AQ	proximal part of right tibia

Al 288-1 (continued)

AR	distal part of right tibia
AS	right astragulus
AT	distal part of right fibula
AU → AZ	rib fragments

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1976 Geological and paleontological background of Hadar hominid site Afar, Ethiopia. Nature 260(5549): 289-293.

C. PROBLEMS IN DATING:

The fossil mammalian fauna

FAUNAL ZONES IN EAST AFRICA

Reference: Coppens, Y. 1972.
C. R. Acad. Sci. 274: 181-184.

Zone VIII	Represented by the fauna from the Lukeino and the Mpesida of the Lake Baringo Basin.
Zone VII	Represented at Lothagam 1 and the Kaperyon Beds, characterized by Stegotetrabelodon Primelephas, Nyanzachoerus archaique, Hippopotamus hexaprotodon, Dinotherium, Stylohipparion, Hipparion Anancus, Australopithecus.
Zone VI	Represented at Kaiso 1 and characterized by the persistence of Primelephas, Hipparion, Anancus, Stegodon, Nyanzachoerus, Hippopotamus hexaprotodon and in the contemporary deposits at Omo 0, Kanapoi, Lothagam 3, Kubi Alga, Chemeron, Kanam, Stegotetrabelodon, Dinotherium, Stylohipparion, Libyatherium and Australopithecus.
Zone V	Represented at Omo (Shungura A, B, C, D); characterized by Stegodon, Nyanzachoerus, Hippopotamus hexaprotodon, Dinotherium, Stylohipparion, Libyatherium, Elephas, Australopithecus and the disappearance of Primelephas and Anancus.
Zone IV	Represented at Omo (Shungura D, E, F, G, lower H); characterized by Hippopotamus hexaprotodon, Dinotherium, Stylohipparion, Libyatherium, Elephas, Australopithecus and the disappearance of Stegodon and Nyanzachoerus.
Zone III	Represented at Olduvai Gorge Bed I and Lower Bed II; characterized by Dinotherium, Stylohiprarion, Libyatherium, Elephas, Australopithecus, Equus and Homo, with the disappearance of Hippopotamus hexaprotodon.

Zone II	Represented at Olduvai Gorge Upper Bed II; characterized by the disappearance of Dinotherium.
Zone I	Characterized by the disappearance of Australopithecus, Stylohipparion and Libyatherium.

MAMMALIAN FAUNA LISTS

EAST AFRICA
(excluding Hominidae)

General reference: Bishop, W.W. 1972: 240-244.

A. ALENGERR BEDS
Age: greater than 12.5 m.y. and less than 14 m.y.

Proboscidea		
	Deinotheriidae	*Deinotherium* c.f. *hobleyi* Andrews
	Gomphotheriidae	
Perissodactyla		
	Rhinocerotidae	*Decerorhinus leakeyi* Hooijer

B. NGORORA FORMATION
Reference: Bishop & Chapman 1970--sediments and fauna described.
Age: probably just less than 12 m.y. or a little younger
(certainly greater than 9 m.y.).

Primates		
	Cercopithecoidea	
Carnivora		
Proboscidea		
	Deinotheriidae	*Deinotherium hobleyi* Andrews
	Gomphotheriidae	
Hyracoidea		sp. nov.?
Perissodactyla		
	Rhinocerotidae	*Chilotherium* sp. *Aceratherium* sp. (?*D. leakeyi* Hooijer) *Brachypotherium* sp.
Artiodactyla		
	Suidae	
	Hippopotamidae	
	Giraffoidea sp.	
	Giraffidae sp.	
Bovidae		
	Boselaphini	*Protragocerus* sp.
	Tragelaphini/Boselaphini sp.	
	Cephalophini/Boselaphini sp.	
	Caprinae/Alcelaphini sp.	

C. MPESIDA BEDS
Reference: Maglio 1970--Elephantidae
Age: 7 ± m.y.

Proboscidea		
	Elephantidae	*Stegotetrabelodon orbus* Maglio
Perissodactyla		
	Equidae	aff. *Hipparion*
	Rhinocerotidae	*Ceratotherium praecox*
Artiodactyla		
	Hippopotamidae	*Hippopotamus* sp.
	Bovidae	

D. LUKEINO BEDS
Reference: Pickford, 1975
Age: 5.4 - 6.7 m.y.

Carnivora		
	Felidae	large sp. small sp.
	Canidae	indet.
	Viverridae	cf. *Ichneumia* sp.
	Hyaenidae	cf. *Crocuta* sp.
	Mustelidae	*Enhydriodon* cf. *iluecai*
Proboscidea		
	Elephantidae	*Stegotetrabelodon orbus* *Primelephas gomphotheroides*
Perissodactyla		
	Equidae	*Hipparion turkanense* cf. *sitifense*
	Rhinocerotidae	2 spp.
	Chalicotheriidae	undet.
Artiodactyla		
	Suidae	*Nyanzachoerus tulotos*
	Hippopotamidae	*Hippopotamus* sp.
	Bovidae	*Reduncini* indet. *Antilopini* indet. *Gazellini* indet. *Neotragini* indet. *Tragelaphini* undet.
	Giraffidae	*Giraffa* cf. *jumae*

E. KAPERYON BEDS
Reference: Maglio 1970: Elephantidae
Age: probably a little older than 5 m.y.

Proboscidea		
	Elephantidae	*Stegotetrabelodon orbus* Maglio *Primelephas gomphotheroides* Maglio
Perissodactyla		
	Equidae	aff. *Hipparion*
Artiodactyla		
	Suidae	
	Hippopotamidae	*Hippoptamus* sp.
	Bovidae	
Rodentia		
	Histricidae	

F. KANAPOI
Reference: Cooke and Maglio 1972.
Age: approximately 4.0 m.y.

Suidae	*Nyanzachoerus* species B *Nyanzachoerus* species A *Notochoerus capensis* *Notochoerus euilus*
Elephantidae	*Loxodonta adaurora* *Elephas ekorensis*

Equidae		Hipparion turkanense
Rhinocerotidae		Ceratotherium praecox

G. LOTHAGAM GROUP I, Levels B and C
Reference: Patterson, Behrensmeyer, Sill 1970, Smart 1976

Primates		
Cercopithecidae		Tribe Papionini cf. Parapapio
		cf. Cercocebus
Carnivora		
Viverridae		? Civettictis
Hyaenidae	aff.	Euryboas
Felidae		subfamily Felinae
		subfamily achairodontinae
Proboscidea		
Deinotheriidae		Deinotherium sp
Gomphotheriidae		subfamily Anancinae
Elephantidae		Stegotetrabelodon orbus
		Primelephas gamphotheroides
Perissodactyla		
Equidae		Hipparion turkanense
		Hipparion sitifense (pygmy)
		Hipparion primigenium
Rhinocerotidae		Brachypotherium lewisi
		Ceratotherium praecox
Artiodactyla		
Suidae		Nyanzachoerus tulotus
	aff.	jaegeri
Hippopotamidae		Hippopotamus (Hexaprotodon) sp. A.
		sp. B.
Giraffidae		Giraffa sp.
Bovidae		Pachytragus like aff. Hippotraginae
	Aff.	Kob[illegible]
	Aff.	Redunca
	Aff	Aepyceros
	Aff	Damaliscus
	Tribe	Hippotragini
		Miotragoceros sp.
		Tragelaphus sp. A
		sp. B
		Gazella sp. A (large)
		sp. B (small)
		Antilope sp.
Tubilidentata		Leptorycteropus guilielmi, gen et sp. nov.
Rodentia		
Anomaluridae		

H. ATERIR BEDS
Reference: Maglio 19[illegible] [illegible]hantidae
Age: [illegible] less than 4 [illegible] ± 0.[illegible] m.y.

Proboscidea	cf.	Anancus sp.
		Mammuthus subplanifrons Osborn

Perissodactyla	
Equidae	aff. *Hipparion*
Rhinocerotidae	*Ceratotherium praecox*
Artiodactyla	
Suidae	c.f. *Sus* sp.
	Nyanzachoerus sp. B
Hippopotamidae	*Hippopotamus* sp.

I. KARMOSIT

Locality discovered and initial collections made by Dr. J.G. McCall.
Age: 3.4 m.y. (or a little older).

Proboscidea	
Perissodactyla	
Rhinocerotidae	
Artiodactyla	
Suidae	*Notochoerus euilus* Hopwood
Hippopotamidae	*Hippopotamus* sp.
Giraffidae	
Bovidae	
Tragelaphini	
Reduncini	
Antilopini	c.f. *Aepyceros* sp.

J. OMO BASIN LAKE TURKANA

References: Beden, 1976. Proboscideans
Butzer, 1971
Cooke and Maglio, 1972
Cooke, 1976. Suidae
Coppens, 1975
Coppens and Howell, 1976
Coryndon and Coppens, 1973
Coryndon, 1976. Hippopotimidae
Eck, 1976. Cercopithecoidea
Eisenmann, 1976. Equidae
Gentry, 1976. Bovidae
Guerin, 1976. Rhinocerotidae, Chalicotheriidae
Hooijer, 1976. Perrissodactyla
Howell and Petter, 1976. Carnivora
Jaeger and Wesselman, 1976. micromammalia

Age: about 4.0 m.y. (Mursi Fm.) to 1.0 m.y. (Upper Shungura Fm.)

Biozonation:	Omo 0= Kaiso 1 "*Hippopotamus* *Protamphibius* zone"	Mursi F. Older than 4.0 m.y.
	Omo 1 "*Elephas recki* stage 1 zone"	Shungura Fm.: Basal member, members A-B-C; Usno Fm. 3.5-2.5 m.y.
	Omo 2	Shungura Fm. members C-D-E-F-G 2.5 m.y. ——— 1.9 m.y

Omo 3	Shungura Fm.
Olduvai Gorge 1	members G-H-J-K-L
	1.9 —— 1.0 m.y.

		Omo 0	Omo 1	Omo 2	Omo 3
Primates					
Cercopithecidae	Papio sp.		X	X	X
	Cercopithecus sp.		X	X	X
	Theropithecus sp. (aff. oswaldi)		X	X	X
	Theropithecus brumpti		X	X	X
	Papionini gen. and sp. indet. A.		X	X	
	Papionini gen. and sp. indet. B.			X	X
	Colobinae gen. and sp. nov.		X	X	X
	Colobinae gen. and sp. indet. A.		X	X	
	Colobinae gen. and sp. indet. C		X	X	X
	Colobus sp.				X
Prosimii	Galago cf. senegalensis		X		
	Galago cf. demidoffi		X		
	Galago sp		X		
Carnivora					
Felidae	cf. Acinonyx sp.	X	X		
	Dinofelis sp.		X	X	X
	Homotherium sp.		X	X	X
	Megantereon sp.		X	X	X
	Panthera pardus		X	X	
	crassidens		X	X	
	leo				X
	Felinae (large) indet.		X	X	
	(small) indet.		X	X	
	Felis (Lynx) caracal		X	X	
Hyaenidae	indet.		X	X	
	Percrocuta sp.		X		
	Hyaena aff. makapani		X	X	
	hyaena			X	X
	Crocuta crocuta			X	X
	Euryboas sp.			X	
Mustelidae	Lutrinae indet.			X	
	Lutra sp.		X		
	Mellivorinae indet. (large)			X	
	Enhydriodon sp. nov.		X	X	
Viverridae	Herpestes sp.			X	
	Viverra leakeyi		X	X	X
	(Civettictis) sp.		X	X	X
	sp.			X	
	Genetta sp. nov.		X	X	
	Helogale sp.		X	X	
	Mungos sp.		X	X	
	Pseudocivetta ingens			X	X

			Omo 0	Omo 1	Omo 2	Omo 3
Proboscidea						
	Elephantidae	Elephas recki st. 1		X	X	
		recki st. 2A		X	X	
		recki st. 2B				X
		recki st. 3				X
		Loxodonta adaurora	X	X	X	
		cf. atlantica			X	
		sp.				X
		Stegodon cf. kaisensis		X		
	Gomphotheriidae	Anancus kenyensis	X			
	Deinotheridae	Deinotherium bozasi	X	X	X	X
Perissodactyla						
	Equidae	Hipparion turkanese	X			
		cf. albertense		X	X	
		ethiopicum		X	X	X
		cf. sitifense			X	X
		Equus sp. (large)			X	X
		sp. (small)				X
	Rhinocerotidae	Ceratotherium praecox	X			
		simum		X	X	X
		Diceros bicornis	X	X	X	X
	Chalicotheridae	Ancylotherium hennigi		X	X	X
Artiodactyla						
	Suidae	Nyanzachoerus jaegeri	X	X		
		Pattersoni	X	X	X	
		kanamensis		X		
		Metridiochoerus jacksoni		X	X	X
		andrewsi		X	X	X
		Notochoerus euilus		X	X	
		capensis		X		
		sp. nov.		X	X	X
		scotti		X	X	X
		Mesochoerus limnetes		X	X	X
		cf. olduvaiensis				X
		Phacochoerus cf. aethiopicus		X	X	X
		antiquus				X
		Stylochoerus nicoli				X
		meadowsi				X
	Hippopotamidae	Hippoptamus sp. nov. D	X	X		
		sp. A		X	X	X
		protamphibius		X	X	
		sp. nov. B.		X	X	X
		gorgops			X	X
	Giraffidae	Giraffa gracilis		X	X	X
		sp. nov.		X	X	X
		cf. jumae		X	X	X
		Sivatherium cf.			X	
		sp.		X		X

		Omo 0	Omo 1	Omo 2	Omo 3
Camelidae	*Camelus* sp.		X	X	X
Bovidae	*Tragelaphus* sp.	X	X	X	
	nakuae		X	X	X
	pricei		X	X	X
	strepsiceres		X	X	X
	Aepyceros sp.	X	X	X	X
	Redunca sp.		X	X	
	Reduncini sp. indet.	X			
	cf. *Connochaetes* sp.		X		
	Oreonagor / *Connochaetes* sp.		X		
	Gazella praethomsoni		X	X	X
	Bovini spp.indet		X	X	X
	alcelaphini spp. indet.		X	X	X
	Kobus ellipsiprymnus			X	X
	sp.		X		
	sigmoidalis		X	X	X
	patulicoruis			X	X
	kob			X	X
	ancystrocera		X	X	X
	Syncerus sp.		X	X	X
	Tauroragus sp.				X
	Antidorcas recki		X	X	X
	Pelorovis sp.				X
	Parmularius/Damaliscus sp.		X	X	
	altidens				X
	Hippotragini sp. indet		X	X	
	Antelope subtorta		X	X	
	Menelikia sp.		X	X	
	lyrocera			X	X
	lyrcera subsp nov.				X
	Pelorovis sp.		X	X	X
	Neotragini spp. indet.			X	X
	Hemibos sp.			X	X
	Megalotragus kattwinkeli			X	X
	Beatragus antiquus				X
Tubulidenta	*Orycteropus* sp.		X	X	
Hyracoidea	*Heterohyrax* sp.		X		
	Gigantohyrax sp.		XX		
Chiroptera	*Eidolon* cf *helrum*		X		
	Taphozous sp.		X		
	Hipposideros sp. A.		X		
	sp. B.			X	
	Coleura sp.			X	
Insectivora	*Crocidura* sp. A.		X		
	sp. B.		X		
	Suncus cf. *infinitesimus*		X		
Lagomorpha	*Lepus* sp.			X	

		Omo 0	Omo 1	Omo 2	Omo 3
Rodentia	*Hystrix* cf. *makapanensis*		X	X	X
	cf. *cristata*			X	X
	Grammomys sp.		X		
	Mus (*Leggada*) sp.		X		
	Lemniscomys sp.		X		
	Xerus erythropus		X		
	Xenohystrix cf. *crassidens*		X		
Seiuridae	indet.		X		
	Pelomys sp.		X	X	
	Paraxerus cf. *ochraceus*		X	X	
	Arvicanthis sp.		X	X	X
	Mastomys cf. *minor*		X	X	X
Muridae	indet.		X	X	X
	Tatera sp.		X	X	X
	Heterocephalus sp.		X	X	
	Thryonomys cf. *swinderianus*		X	X	X
	cf. *Oenomys* sp.		X	X	
	Aethomys sp.			X	
	Xerus sp.			X	
	Thallomys sp. *quadrilobatus*			X	
	Gerbillurus sp.			X	
	Dendromus sp.			X	
	Jaculus cf. *orientalis*			X	

K. HADAR FORMATION, Central Afar, Ethiopis
Reference: Taieb, Johanson, Coppens, Aranson, 1976.
Age: 3.0 m.y.

Primates	
Cercopithecidae	*Papio* sp.
	Theropithecus sp.
	Colobus sp.
Carnivoar	
Canidae	Gen. et sp. indet.
Hyaenidae	*Crocuta* sp.
Mustelidae	? *Enhydriodon* sp.
	gen. et sp. indet.
Felidae	*Megantereon* sp.
	? *Dinofelis* sp.
Artiodactyla	
Hippopotamidae	*Hippopotamus* cf. *imagunculus*
Suidae	*Sus* sp.
	Notochoerus cf. *euilus*
	Nyanzachoerus pattersoni

Giraffidae	Sivatherium maurasium
	Giraffa cf. jumae
	Giraffa sp. nov.
Bovidae	Ugandax sp.
	Tragelaphus cf. nakuae
	Tragelaphini gen. et sp. indet.
	Hippotragus sp.
	Kobus sp.
	Aepyceros sp.
	aff. Parmularis sp.
	Alcelaphini gen et sp. indet.
	Neotragini/Cephalophini gen. et sp. indet.
	Ovibovini gen et sp. indet.
Perissodactyla	
Equidae	Hipparion cf. primigenium
	Hipparion sp.
Rhinoceratidae	Ceratotherium cf. praecox
	Diceros cf. bicornis
Proboscidea	
Elephantidae	Elephas recki
	? Elephas sp.
	Loxodonta cf. adaurora
	Primelephas sp.
Deinotheroidea	
Deinotheridae	Deinotherium bozasi
Rodentia	Hystrix sp.
	Mastomys sp.
	Xenohystrix cf. crassidens
	Xerus sp.
	Tachyoryctes sp.
	Pelomys sp.
	Oenomys sp.
	Tatera sp.

L. CHEMERON FORMATION

References: Martyn 1967 -- sediments (including comments on fauna by L.S.B. Leakey)
Leakey, R.E.F. 1969 Cercopithecidae
Hooijer 1969, 1972, 1973, Rhinocerotidae
Maglio 1970 -- Elephantidae

Age: greater than 2.0 m.y. and less than 5.4 m.y.

Primates	Papio baringensis Leakey
	Paracolobus chemeroni Leakey
Proboscidea	Deinotherium bozasi Arambourg

		Anancus sp.
		Mammuthus subplanifrons Osborn
		Loxodonta adaurora Maglio
		Elephas recki stage 2 Dietrich
Perissodactyla		
Equidae	aff.	*Hipparion*
Rhinocerotidae		*Ceratotherium praecox*
		C. simum
		Ancylotherium hennigi
		Chalicotheriidae
Artiodactyla		
Suidae		*Nyanzachoerus* sp. 'A'
		Nyanzachoerus sp. 'B' or *Mesochoerus*
		c.f. *heseloni* Leakey
	c.f.	*Mesochoerus* sp.
	c.f.	*Sus* sp.
	c.f.	*Potamochoerus* sp.
Hippotamidae		*Hippopotamus* c.f. *imagunculus* Hopwood
		Hippopotamus sp. nov.
Giraffidae		
Sivatheriinae		
Bovidae		
Tragelaphini		
Alcelaphini		
Rodentia		
Hystricidae		c.f. *Xenohystrix crassidens*

M. EAST LAKE RUDOLF

Reference: Eisenmann 1976. Equidae
Harris 1976. Bovidae
Harris 1976. Rhinocerotidae
Harris 1976. Giraffidae
Leakey, M. 1976. Cercopithecoidea
Leakey, M. 1976. Giraffidae
Maglio 1972

Age: Radiometric determinations of the KBS Tuff are being revised. Dates range from 2.6 m.y. to 1.5 m.y.

Biozonation:

Zone 4 "*Notochoerus capensis* Zone". Represented at the Kubi Algi Fm. and characterized by *Elephas ekorensis*, *Notochoerus capensis*, *Nyanzachoerus* sp. and early *Hippopotamus* sp.

Zone 3 "*Mesochoerus limnetes* Zone". Represented at the Lower Member, Koobi Fora Formation and characterized by *Elephas recki* stage 2, *Notochoerus euilus* (progressive), *Mesochoerus limnetes* (typical), *Ceratotherium simum* (early), *Hippopotamus* sp. nov. (early), and *Tragelaphus nakuae*

Zone 2 "*Metridiochoerus andrewsi* Zone". Represente in the Upper member at Koobi Fora Fm. at levels between the KBS and Koobi Fora Tuffs, and in the Ileret member of the Koobi Fora Fm. between the KBS and Lower tuffs. Characterized by *Elephas recki* stage 3, *Mesochoerus limnetes* (progressive), *Metridiochoerus andrewsi* (typical), *Hippopotamus* sp. nov. (typical), *Ceratotherium simum* (progressive), *Tragelaphus* cf. *grandis*.

Zone 1 "*Loxondonta africana* Zone". Represented in the Ileret Member of the Koobi Fora Fm. between the Lower and Chari tuffs. Characterized by *Elephas recki* stage 3-4, *Loxodonta africana*, *Mesochoerus limnetes* (very progressive), *Metridiochoerus andrewsi* (progressive), *Hippopotamus* cf. *amphibius*, *Ceratotherium simum* (very progressive).

			Ileret	Koobi Fora	Kubi Alga
Primates					
	Cercopithecidae	*Cercocebus* cf. *ado*	X	X	
		Cercopithecus sp. indet.	X	X	
		Colobus sp.	X	X	
		Colobinae gen et sp. indet.		X	
		cf. *Papio* sp.		X	
		Simopithecus sp.	X	X	
Carnivora					
	Hyaenidae	*Crocuta* cf. *crocuta*	X	X	
		Hyaena cf. *hyaena*	X	X	
	Canidae	*Canis* cf. *mesomeles*	X	X	
	Felidae	*Panthera* sp.	X	X	
		cf. *Therailurus* sp.	X		
		cf. *Homotherium* sp.		X	
		Megantereon eurynodon	X	X	
	Mustelidae	*Lutra* sp.	X	X	
	Viverridae	gen et sp. indet.	X		
Proboscidea					
	Deinotheriidae	*Deinotherium bozasi*	X	X	
	Elephantidae	*Elephas ekorensis*			X
		Elephas recki stage 2,3	X	X	
		Loxondonta adaurora		X	X
		Loxondonta africana	X		
	Gomphotheriidae	*Anancus* sp.			X
Perissodactyla					
	Equidae	*Equus* sp.	X	X	
		Hipparion cf. *sitifense*	X	X	

		Ileret	Koobi Fora	Kubi Alga
Rhinoceratidae	*Ceratotherium simum*	X	X	
	Diceros bicornis	X	X	
Artiodactyla				
Bovidae	*Damaliscus* sp. nov.	X	X	
	Damaliscus cf. *niro*	X	X	
	Connochaetes cf. *africanus*	X		
	Megalotragus cf. *kattwinkeli*	X	X	
	Aepyceros sp.	X	X	
	Antidorcas wellsi		X	
	Gazella sp. indet.		X	
	Pelorovis cf. *olduwavensis*	X		
	Pelorovis sp. nov.	X	X	
	cf. *Synceros* sp.			X
	Hippotragus gigas	X		
	Oryx sp.	X		
	Kobus sigmoidalis	X	X	
	Kobus cf. *kob*	X	X	
	Menelikia sp.	X	X	
	Redunca ancystocera	X	X	
	Tragelaphus nakuae		X	
Giraffidae	*Sivatherium* sp.nov.	X	X	
	Giraffa cf. *jumae*	X	X	
	Giraffa sp.(=cf. *stillei*)	X	X	
	Giraffa cf.*gracilis*	X	X	
Suidae	*Mesochoerus limnetes*	X	X	
	Metridiochoerus andrewsi	X	X	
	"*Pronotochoerus jacksoni*"	X	X	
	Notochoerus capensis			X
	Notochoerus euilus		X	
	Notochoerus scotti		X	
	Nyanzachoerus sp.			X
	Potamochoerus sp.	X		
	Phacochoerus cf. *aethiopicus*	X	X	
	cf. *Afrochoerus nicoli*		X	
Hippopotamidae	*Hippopotamus* sp. nov.	X	X	
	Hippopotamus cf. *amphibius*	X	X	
	Hippopotamus aff. *imagunculus*	X	X	X
Tubulidentata				
Orycteropodidae	*Orycteropus* sp.	X	X	
Rodentia				
Hystricidae	*Hystrix* sp.	X		
Thryonomyidae	*Thryonomys* sp.	X	X	

N. OLDUVAI GORGE

Reference: M. Leakey 1971
Age: less than 1.9 m.y.

			Bed I		Bed II
			lower	upper	lower
Primates					
	Lorisidae	*Galago senegalensis*		X	
		Galago sp.	X		
	Cercopithecidae	*Simopithecus* cf. *oswaldi*	X	X	
		c.f. *Cercocebus* sp.	X		
		Papio sp.		X	
		Colobus sp.		X	
	Indet.				X
Insectivora					
	Erinaceidae	*Erinaceus broomi*		X	
	Macroscelididae	*Nasilio* sp.		X	
		? *Elephantulus* sp.		X	
		Indet.		X	
	Indet.			X	X
	Soricidae	*Mysorex* cf. *robinsoni*		X	
		Crocidura cf. *hindei*		X	
		Suncus sp.		X	
		Suncus cf. *lixus*		X	
		Suncus cf. *orangiae*		X	
Chiroptera					
	Megadermidae	Indet.			
	Vespertilionidae	Indet.		X	
Carnivora (reference: Petter 1973)					
	Canidae	*Canis mesomelas*		X	
		Prototocyon recki		X	
	Mustelidae	*Aonyx* sp.	X	X	
	Viverridae	*Herpestes* sp. aff. *ichneumon*		X	
		Galerella primitivus sp. nov.		X	
		Galerella debilis sp. nov.		X	
		Atilax sp.			X
		Ichneumia sp. aff. *albicanda*		X	
		Mungos dietrichi		X	
		Mungos minutus sp. nov.		X	
		Mungos sp.		X	
		Pseudocivetta ingens	X	X	
		Pseudicivetta ingens s. sp.			
	Hyaenidae	*Crocuta crocuta*	X	C	X
		Hyaena hyaena		X	X

		Bed _		
		lower	upper	
Felidae	Panthera leo s. sp		X	X
	Panthera pardus s. sp.		x	
	Panthera crassidens			
	? Machairodus sp.			
	? Metailurus sp.			
Proboscidea				
Deinotheriidae	Deinotherium cf. bozasi	X	X	
Elephantidae	Elephas recki stage 3		X	
Hyracoidea				
Procavidae	Indet.	X		
Perissodactyla				
Equidae	Equus cf. olduwayensis	X	X	X
	Stylohipparion sp.	X	X	X
Chalicotheriidae	Ancylotherium cf. hennigi	X		
Rhinocerotidae	Ceratotherium simum	X	X	X
	Diceros bicornis			X
Artiodactyla				
Suidae (reference: Cooke and Maglio, 1972)				
	Mesochoerus olduvaiensis			
	Mesochoerus dubius		X	
	Phacochoerus antiquus		X	
	Pronotochoerus jacksoni		X	
Hippopotamidae	Hippopotamus gorgops	X	X	
Giraffidae	Giraffa jumae		X	
	Giraffa gracilis			
	Giraffa sp.	X	X	
	Okapia sp.	X	X	
	Libyatherium olduvaiensis	X	X	X
Bovidae	Strepsiceros maryanus	X	X	X
	grandis			X
	Strepsicerotini indet.	X	X	X
	Pelorovis oldowayensis			X
	Bovini (small) indet.	X	X	X
	Kobus sigmoidalis		X	
	Kobus sp.	X	X	X
Redunca sp.		X		
	Hippotragus gigas	X	X	X
	Oryx sp.		X	
	Hippotragini indet.		X	X
	Parmularius altidens	X	X	
	Xenocephalus sp.	X		
	Beatragus antiquus		X	
	Gorgon olduvaiensis		X	
	Damaliscus angusticornis		X	
	Damaliscus niro			
	Alcelaphini indet.	X	X	
	Neotragini indet.		X	
	Gazella wellsi	X	X	
	Phenacotragus recki			X
	Gazella sp.			X

		Bed I lower	Bed I upper	[illegible]
	Antilopini indet.	X		X
	Pultiphagonides africanus			X
	Tribe indet. sp. nov.		X	
Rodentia				
Cricetidae	*Tatera* sp.		X	
Muridae	*Otomys kempi*		X	
	Gerbillus sp.		X	
	Saccostomus sp.		X	
	cf. *Grammomys* sp.		X	
	cf. *Steatomys* sp.		X	
	Dendromys sp.		X	
	Various		X	
Sciuridae	*Xerus* sp.		X	
Pedetidae	*Pedetes* sp.		X	
Hystricidae	*Hystrix* sp.	X	X	X
Bathyergidae	*Hetercocephalus* sp.		X	
Lagomorpha				
Leporidae	*Serengetilagus* sp.		X	

O. CHESOWANJA (Chemoigut Formation)

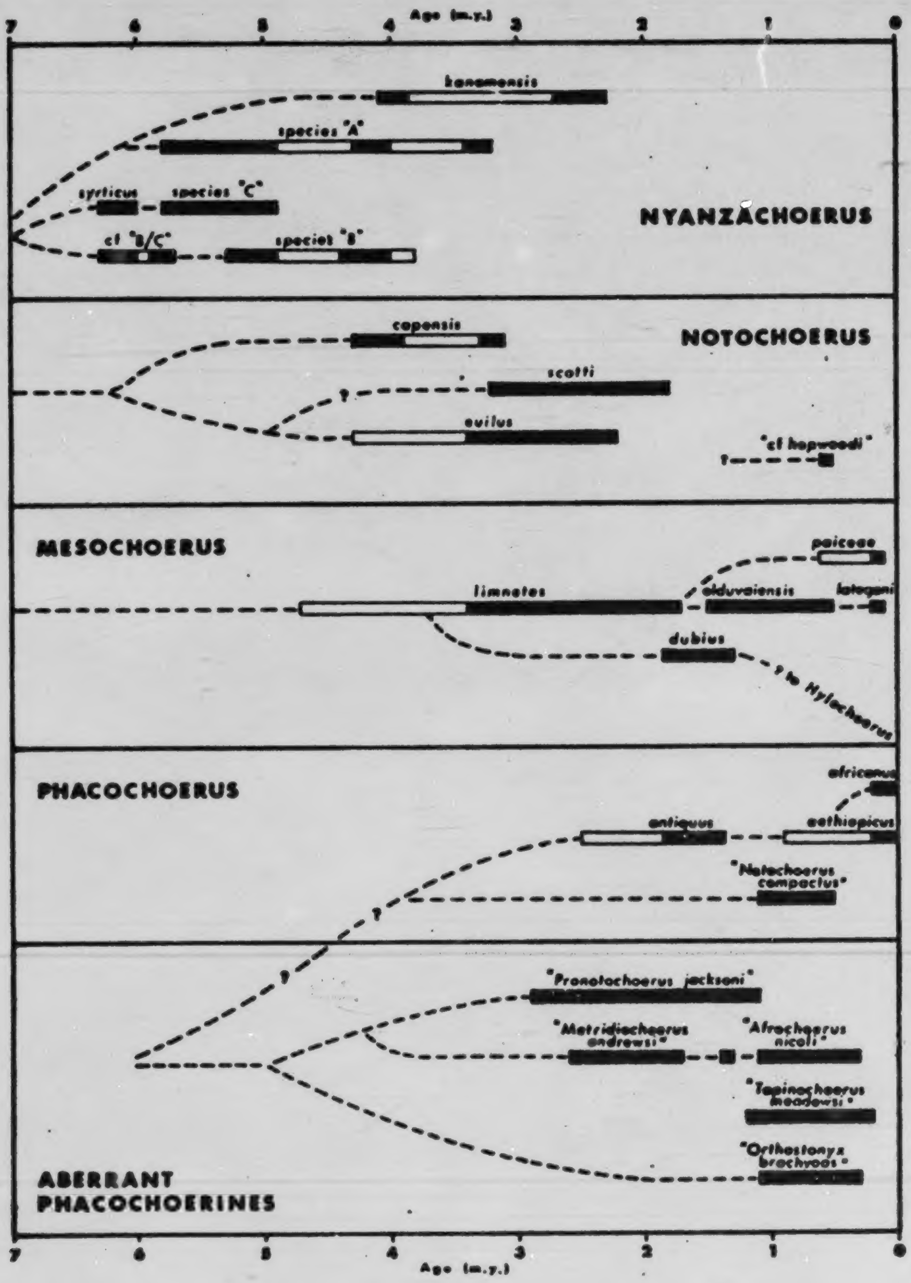
Reference: Bishop, Pickford and Hill, 1975
Age: Somewhat in excess of 1.34 m.y.

Primates	
Cercopithecidae	*Simopithecus* sp.
	sp indet.
Proboscidea	
Elephantidae	*Elephas* c.f. *recki* Dietrich
Deinotheriidae	*Deinotherium bozasi* Arambourg
Perissodactyla	
Equidae	*Equus* sp.
Rhinocerotidae	*Ceratotherium* sp.
Artiodactyla	
Suidae	*Mesochoerus* sp.
	Metridiochoerus andrewsi
	Metridiochoerus jacksoni
	+ 2 other species
Hippopotamidae	*Hippopotamus* c.f. *amphibius* Linn
	Hippopotamus sp.
Giraffidae	
Bovidae	
Tragelaphini	*Tragelaphus* sp.
? Tragelaphini	
Bovini	
Reduncini	*Kobus* sp.
Alcelaphini	? *Megalotragus kattwinkeli* Schwarz

	? *Connochaetes* sp.
	small sp.
	smaller sp.
Antilopini	? *Antidorcas* sp.

EVOLUTION OF FOSSIL SUIDAE IN AFRICA

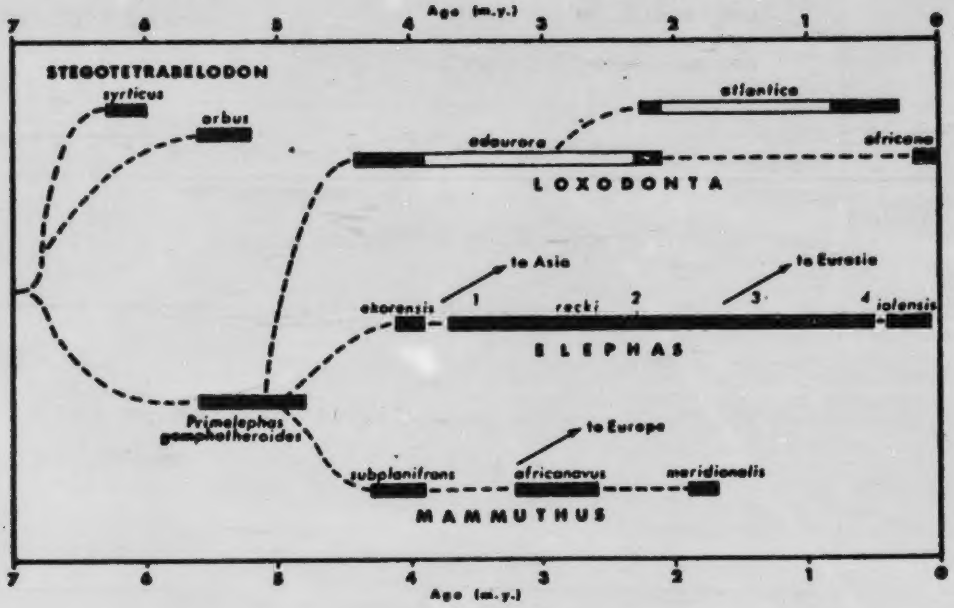
Figure 11-32



From Cooke and Maglio (1972): 308.

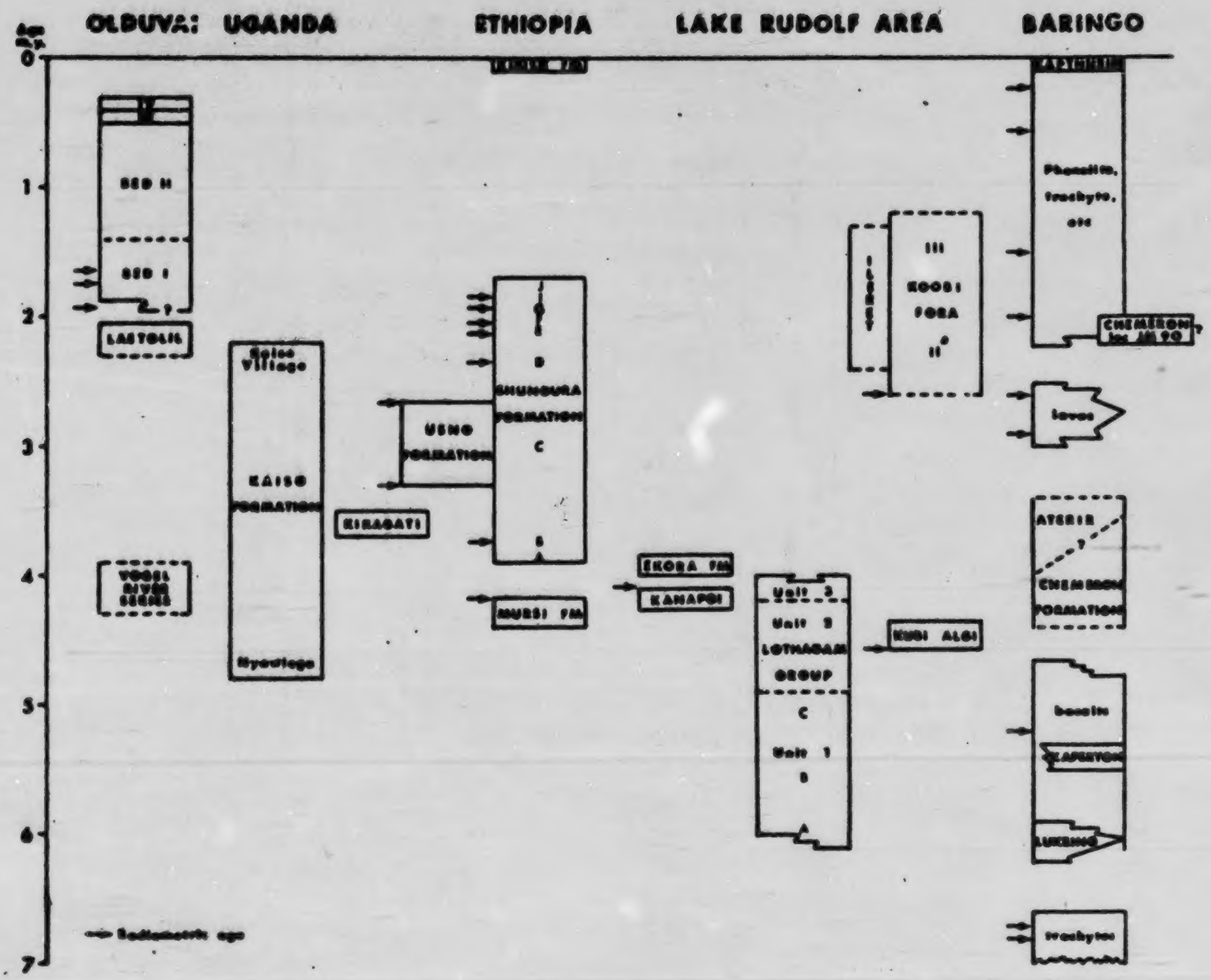
EVOLUTION OF FOSSIL ELEPHANTIDAE IN AFRICA

Figure II-33


Age (m.y.)
7
6
5
4
3
2
1
0
STEGOTETRABELODON
syrticus
orbus
atlantica
adaurora
africana
LOXODONTA
to Asia
to Eurasia
ekorensis
1
recki
2
3
4
iolensis
ELEPHAS
Primelephas gomphotheroides
to Europe
subplanifrons
africanavus
meridionalis
MAMMUTHUS
7
6
5
4
3
2
1
0
Age (m.y.)

From Cooke and Maglio (1972): 319.

Figure 11-34

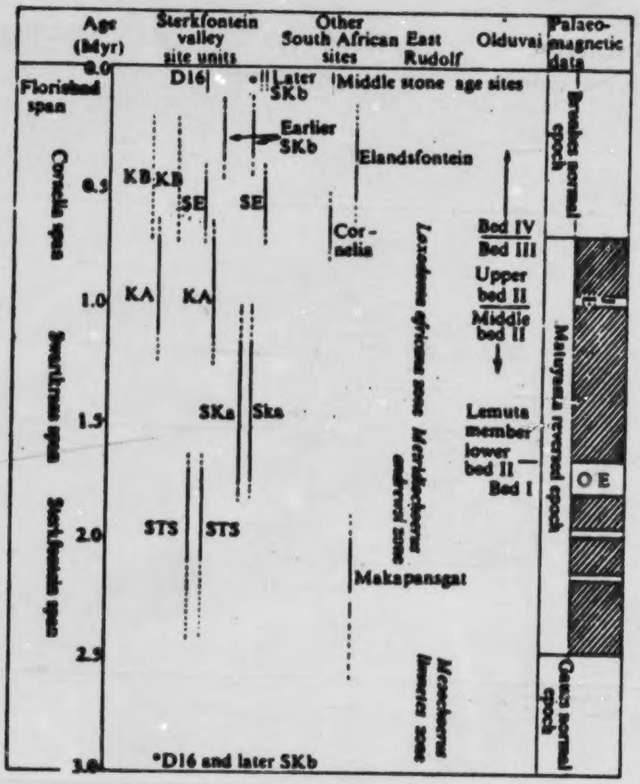


TENTATIVE CORRELATIONS OF PLIO/PLEISTOCENE DEPOSITS IN EAST AFRICA BASED ON PROBOSCIDEA AND SUIDAE.

(From Cooke and Maglio (1972): 306)

Figure 11-35

Biostratigraphy of Fossil Hominid Bearing Sites in South Africa



Chronological relationships of the hominid bearing sites in South Africa based on the data of fossil bovids. Comparative data from East Rudolf and Olduvai Gorge, East Africa included.
J.E. = Jaramillo Event
O.E. = Olduvai Event
(From Vrba (1975):303)

MAMMALIAN FAUNAL LISTS

SOUTH AFRICA
(excluding Hominidae)

General Reference: Brain 1958
Annals of Transvaal Museum 11: 129-130.

STERKFONTEIN TYPE SITE (STS)

Age: Sterkfontein Faunal Span, about 2.0 ± .5 million years.

Insectivora	
Myosorex robinsoni Meester	Meester, 1955
Suncus Hemprich and Ehrenberg *sp.*	"
Chlorotalpa spelea Broom	Broom, 1941
Elephantulus Thomas & Schwann *sp.* possibly = *E. langi* Broom	Broom & Schepers, 1946
Primates	
Parapapio jonesi Broom	Freedman, 1957
Parapapio jonesi Jones	"
Parapapio whitei Broom	"
Cercopithecoides williamsi Mollet	"
Proboscidea	
Elephantidae	
Elephas ekorensis	Maglio, 1972
Carnivora	
Hyaena Brisson *sp.*	Ewer, 1955a
Crocuta cf. *spelaea* (Goldf.)	"
Lycyaena silberbergi Broom	Ewer, 1955b
? *Lycyaena nitidula* Ewer	"
Therailus barlowi (Broom)	Ewer, 1955c
Megantereon gracile Broom	Broom, 1948
? *Panthera pardus* (Linn.)	Ewer, 1956b
Canis mesomelas Schreber sub-sp. *pappos* Ewer	"
Hydracoidea	
Procavia transvaalensis Shaw	Churcher, 1956
Procavia antiqua Broom	"
Artiodactyla	
Tapinochoerus meadowsi (Broom)	Ewer, 1956c
Metridiochoerus andrewsi	Maglio, 1972
Bovidae (reference: Vrba 1974)	
Hippotragus cf. *equinus*	
cf. *Megalotragus* sp.	
Redunca cf. *arundinum*	
Syncerus cf. *acoelotus*	
Tragelaphus sp. aff. *angasi*	
cf. *Gazella vanhoepeni*	

Makapania cf. *broomi*
cf. *Hippotragus* sp. aff. *gigas*
Oreotragus major
Antidorcas cf. *recki*
Antidorcas bondi ?
Taurotragus cf. *oryx* ?
Connochaetes taurinus lineage
Damaliscus sp.
medium-sized alcelaphines

Rodentia

Mystromys hausleitneri Broom (Broom 1948 puts this in a separate subspecies, *barlowi*, distinct from the Kromdraai form, but Lavocat 1956 does not think the separation is justified)	Broom, 1948
Cryptomys robertsi Broom	Broom & Schepers, 1946
Palaeotomys Broom *sp.*	Lavocat, 1957
Dendromus Smith *sp.*	"
Dasymys Peters *sp.*	"
? *Arvicanthis* Lesson *sp.*	"
Mus minutoides Smith	"
Tatera Lataste *sp.*	"

MAKAPAN LIMEWORKS DEPOSIT

Age: Sterkfontein Faunal Span, about 2.0 million years and earlier.

Insectivora

Myosorex robinsoni Meester	Meester, 1955
Suncus Hemprich & Ehrenberg *sp.*	"

Primates

Parapapio jonesi Broom	Freedman, 1957
Parapapio broomi Jones	"
Simopithecus darti (Broom & Jensen)	"
Cercopithecoides williamsi Mollet	"

Carnivora

Hyaena makapani Toerien	Toerien, 1952
Crocuta cf. *brevirostris* (Aym.)	"
Machaerodus darti Toerien = *Therailuris barlowi* (Broom) according to	Toerien, 1955 Ewer, 1956a
Felidae indet.	"
Canis cf. *adustus* Sundevall	Ewer, 1956c
Vulpes Frisch *sp.*	"
Cynictis penicillata (G. Cuv.) sub-sp. *brachydon* Ewer	Ewer, 1956d

Hydracoidea

Procavia transvaalensis Shaw	Churcher, 1956
Procavia antiqua Broom	"

Perissodactyla	
Stylohipparion van Hoepen sp.	Wells & Cooke,1956
Metaschizotherium (?) transvaalensis George	George,1950
? Ceratotherium Gray sp.	Wells & Cooke,1956
Diceros cf. bicornis (Linn.)	"
Artiodactyla	
Potamochoerides hypsodon Dale	Ewer,1958
Potamochoerides shawi (Dale)	"
Notochoerus euilus (Hopwood)	"
Notochoerus scotti	Maglio,1972
Bovidae (reference: Vrba 1974)	
? Redunca cf. arundinum	
? Syncercus cf. acoelotus	
? Tragelaphus sp. aff. angasi	
cf. Gazella vanhoepeni	
Makapania cf. broomi	
Hippotragus sp. aff. gigas	
Oreotragus major	
Hippopotamus makapanensis Kitching =	Kitching,1951
H. cf. amphibius Linn. according to	Wells & Cooke, 1956
Giraffa cf. camelopardus Linn.	"
Griquatherium cf. cingulatum Haughton	"
Strepsiceros cf. strepsiceros (Pallas)	"
Strepsiceros (Tragelaphus) cf. angasi (Gray)	"
Taurotragus cf. oryx (Pallas)	"
cf. Syncerus caffer (Sparrman)	"
Cephalopus pricei Wells & Cooke	"
cf. Cephalopus (Guevei) caerulus (Hamilton Smith)	"
Redunca darti Wells & Cooke	"
Redunca cf. fulvorufula (Afzelius)	"
cf. Oryx gazella (Linn.)	"
Damaliscus sp. (aff. albifrons (Burchell))	"
cf. Gorgon taurinus (Burchell)	"
cf. Alcelaphus robustus Cooke	"
cf. Pelorocerus helmei (Lyle)	"
Makapani broomi Wells & Cooke	
Oreotragus major Wells	
Aepyceros cf. melampus (Lichenstein)	"
Gazella gracilior Wells & Cooke	"
Phenocotragus vanhoepeni Wells & Cooke	"
Rodentia	
Gypsorhyncus makapani Broom	Broom,1948
Xenohystrix crassidens Greenwood	Greenwood,1955
Hystrix major Greenwood	"
Hystrix cf. africae-australis Peters	"
Mystromys darti Lavocat	Lavocat,1956
Mystromys hausleitneri Broom	Lavocat,1957
Heterocephalus Ruppell sp.	"
Palaeotomys gracilis Broom	"
Malacothrix Wagner sp.	"
Dendromus Smith sp.	"

Dasymys Peters *sp.*	Lavocat, 1957
Pelomys (?) Peters *sp.*	"
Lemniscomys (?) Trouessart *sp.*	"
Zelotomys (?) Osgood	"

SWARTKRANS (SKa) Member 1 of the Swartkrans Formation (Brain, 1976)
Age: Swartkrans Faunal Span, about 1.5 ± .5 million years.

Insectivora	
Myosorex robinsoni Meester	Meester, 1955
Suncus Hemprich & Ehrenberg *sp.*	"
Primates	
Parapapio jonesi Broom	Freedman, 1957
Papio robinsoni Freedman	"
Simopithecus danieli Freedman	"
Dinopithecus ingens Broom	"
Cercopithecoides molleti Freedman	"
Hydracoidea	
Procavia transvaalensis Shaw	Churcher, 1956
Procavia antiqua Broom	"
Carnivora	
Octocyon recki Pohle	Hendey, 1974
Mellivora cf. *sivalensis* Falconer and Cautley	"
Herpestes cf. *sanguineus* Ruppell	"
Proteles transvaalensis spec. nov.	"
Proteles cristatus Sparrman	"
Euryboas silberbergi Broom	"
Dinofelis cf. *barlowi* Cooke	"
Hyaenictis forfex = *Leecyaena* Ewer	Ewer, 1955a
Hyaena brunnea Thunb. sub-sp. *dispar*. Ewer	"
Crocuta venustula Ewer	"
Crocuta crocuta (Erxl.) sub-sp. *angella* Ewer	"
Lycyaena silberbergi Broom	Ewer, 1955b
Lycyaena nitidula Ewer	"
Therailurus Piveteau *sp.*	Ewer. 1955c
Megantereon Cr. & Job. *sp.*	"
Nimravidae indet.	"
Panthera pardus (Linn.) sub-sp. *incurva* Ewer	Ewer, 1956b
Panthera aff *leo*	Hendey, 1974
Canis mesomelas Schreber sub-sp. *pappos*	Ewer, 1956c
Vulpes sp. ? = *V. pulcher* Broom	"
Cynictis penicillata Cuvier	Ewer, 1956d
? = sub-sp. *brachydon* Ewer	Ewer, 1956a
Lycaon sp. indet.	Hendey, 1974
Artiodactyla (suidae)	
Tapinochoerus meado[illegible] Broom	Ewer, 1956c
Phacochoerus antiquus Broom	"

Bovidae	
? Damaliscus porrocornutus Vrba	Vrba, 1971
Damaliscus sp. 1 (*Parmularius* sp.)	Brain, 1976
Rabaticeras porrocornutus	"
Beatragus sp.	"
cf. *Connochaetes taurinus*	"
cf. *Megalotragus* sp.	"
? Hippotragini	"
Redunca cf. *arundinum* (*darti?*)	"
Pelea capreolus	"
Antidorcas cf. *recki*	"
? *Gazella* sp	"
Oreotragus cf. *minor*	"
Syncerus sp	"
Tragelaphus cf. *strepsiceros*	"
cf. *Makapania* sp.	"
Equidae	
Equus capensis	"
Equus quagga	"
Hipparion steyleri	"
Hyracoidae	
Procavia transvaalensis	"
Procavia antiqua	"
Lagomorphidae	
Hystrix africae-australis	"

KROMDRAAI FAUNAL SITE

Age: Latest Swartkrans Faunal Span -- Cornelia Faunal Span, about 1.0 million years and later.

Kromdraai A	
Insectivora	
Suncus Hemprich & Ehrenberg *sp*	Maester, 1955
Chrysochloris, possibly *Proamblysomus antiquus* Broom	Broom, 1948
Primates	
Parapapio jonesi Broom	Freedman, 1957
Papio robinsoni Freedman	"
Papio augusticeps Broom	"
Gorgopithecus major Broom & Robinson	"
Carnivora	
Crocuta spelaea (Goldfuss) sub-sp. *capensis* Broom	Ewer, 1954
Crocuta ultra Ewer	"
Hyaena bellax Ewer	"
Therailurus piveteaui Ewer	Ewer, 1955c
Megantereon eurydodon Ewer	"
? *Epimachairodus* Kretzoi *sp*.	"
Felis crassidens Broom	Broom, 1948
Kromdraai "lion" ? = *Panthera shawi* (Broom)	Ewer, 1956b
Canis mesomelas Schreber sup-sp. *pappos* Ewer	Ewer, 1956c
Canis atrox Broom	Broom, 1939 & 1948
Vulpes pulcher Broom	Broom, 1937
Herpestes mesotes Ewer	Ewer. 1956d
? *Crossarchus transvaalensis* Broom	Broom, 1939
Hydracoidea	
Procavia transvaalensis Shaw	Churcher, 1956
Procavia antiqua Broom	"
Perissodactyla	
Equus sp. probably *E*. *zietsmani* Broom	Broom, 1948
Artiodactyla	
Phacochoerus antiquus Broom	Ewer, 1956c
Rodentia	
Mystromys hausleitneri Broom	Broom, 1948 Lavocat, 1956
Kromdraai B	
Carnivora	
Canidae	
Species incertae sedis (? two species)	Hendey, 1973
? *Canis mesomelas*	"
Canis terblanchei	"
Viverridae	
Species incertae sedis	Hendey, 1973
Herpestes sp.	"
Hyaenidae	
Hyaena cf. brunnea Thunberg	Hendey, 1973
Proteles sp.	"

Felidae	
? *Megantereon sp.*	Hendey, 1973
? *Panthera pardus*	"
Primates	
Cercopithecoides williamsi Mollett	Freedman and Brain, 1972
Papio robinsoni Freedman	"
Papio augusticeps Broom	"

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D. PROBLEMS IN INTERPRETATION

The post-cranial and endocranial evidence.

EVIDENCE FROM THE POST CRANIAL MATERIAL

A comparison of the lists of hominid remains clearly demonstrates that the post cranial material is rather poorly represented in existing collections, but in general, most anatomists agree that the early hominids were both upright in posture and bipedal rather than quadrupedal in gait.

Computation of stature of the australopithecines has used those techniques determined successful on modern populations. Until the Afar hominids and KNM-ER 803 have been fully described, the single most complete specimen is STS 14, which includes all six lumbar vertebrae, sacrum, several ribs, femur, as well as the reconstructed pelvis. The small size and slender construction of the bones suggest a small-sized individual. Robinson (1972: 231) has estimated the height of this specimen based on the ratio between the sum of the lumbar vertebrae body lengths and stature in modern populations as well as estimated femur length. These estimates range from slightly below 4 feet (122cm) to 4 feet 6 inches (137cm). Much lower estimates ranging between 107-109cm (3'6"-3'7") have been calculated by Lovejoy and Heiple (1970) for the gracile australopithecines based on a reconstruction of the STS 14 femur alone.

The evidence for the robust australopithecine is not as substantial for estimating stature, the Swartkrans innominate (SK 50) measures approximately 22% larger than that of STS 14 (Robinson 1972: 234). The Kromdraai innominate is of comparable size. Day (1973: 32-33) reviewed the anatomical evidence of SK 50 and SK 3255b and believed that the acetabulum was small, that there was some backward extension of the ilium, that there was a marked area of attachment for the Rectus femoris muscle with evidence of a reflected head, and that there was a marked ilio-psoas groove medial to the anterior inferior iliac spine. He states, however, that because of the condition of the SK 50 specimen all anatomical measurements should only be considered approximate.

There are no long bones of the robust australopithecines from South Africa sufficiently complete to provide an estimate of stature. The two femora from Swartkrans (SK 82, SK 97), however, are considerably more robust than the ones from Sterkfontein. Robinson (1972: 235) has suggested that by comparing the percentage differences in the post cranial bones that the robust form was slightly taller and perhaps moderately heavier. Estimates range from 4'6" (137 cm) to 5' (152 cm) in height and as much as 150-200 pounds in weight. The vertebrae suggest that the gracile males and the robust females may have been about the same size.

Burns (1971), using a ratio between femoral head diameter and body height of modern Homo sapiens, determined that body height could be calculated by the equation, Stature= 13.29 x femoral head diameter + 108.59 cm. Using this equation, the height of SK 82 was determined to be 151 cm and that of SK 97 as 157 cm. Both estimates are within the range proposed by Robinson.

More recently, McHenry (1974) has proposed new height estimates based on regression analysis. He claims that values derived from the forelimb and hindlimb should not necessarily coincide since the limb proportions in australopithecines were probably different than in the modern forms. Estimates based on femora STS 14 and STS 34 yield a range between 4'3" (131 cm) and 4' 10" (147 cm). If the STS humerus is included in the sample, the uppermost limit of the range is increased to 5'3" (159 cm). McHenry presumes that this variability in stature is related to sexual dimorphism. On the small sample of postcrania from Swartkrans and Kromdraai, the published range is much smaller from 4'10" (148 cm) to 5'2" (157 cm). Comparisons of single bones, the humeri STS 7 and TM 1517, of different populations indicate how much size overlap exist between the South African forms.

Calculations of stature on the recently recovered femoral remains from East Africa, KNM-ER 736, 737 and 738, have yielded much more valuable estimates. For the one species of Australopithecus represented by KNM-ER 738, and 736, the range is respectively 4'11" (149 cm) to 6'1" (186 cm). Specimen KNM-ER 737, attributed to the genus Homo, was estimated in height at 5'6" (168 cm). McHenry concludes that over time (from 4.0 to 1.3 m.y.) a trend of increasing size is discernible. Estimates have also been given for body weight and have varied among the different hominid forms from 40 lbs (Lovejoy and Heiple 1970) to 200 lbs (Robinson 1972). New techniques have attempted to relate skeletal size to body weight in both modern humans and great apes. By calculating regression formulas, more accurate predictions have been made for the fossil forms. It has been demonstrated that high correlations exist between the cross-sectional area of the vertebral centra and the live weight of the specimen. This same positive correlation exists between the proximal femur size and body weight. Calculating estimates based on the vertebral formula for STS 14 of 61 lbs (27.6 kg) and for SK 3981 of 79 lbs (36.1 kg) provides a lower limit for both the gracile and robust australopithecines. The upper limits have been found for the gracile form STS 13 at 95 lbs (43.0 kg) and for the robust form based on the proximal femur at 116 lbs (57.7 kg).

LOWER LIMBS

Of the bones of the lower limb, the femur is certainly the best represented. The two femoral fragments from Swartkrans (SK 82, SK 97), the femur from Olduvai (OH 20), and more recently a right proximal fragment from Hadar (AL 211-1) show similar morphological features in that the first three display a groove for the obturator externus tendon on the posterior side of the femoral neck which functions in hyperextension and extension of the hip joint. Identification of an additional groove on the anterior aspect of the femoral neck for the tendon of the ilio-psoas muscle confirms that hip extension was habitual rather than occasional (Day 1973: 35-36).

Certain features of the robust australopithecine femora are, however, unique. The combination of a small head, long and relatively flat (antero-posteriorly compressed) neck, non-flared greater trochanter, posteriorly directed lesser trochanter, rather high femoro-condylor angle, and stout, short shaft differs from living groups (Day, 1973: 36). Most of this diagnosis is confirmed by Lovejoy and Heiple (1972), who also demonstrate that the presence of the inter-trochanteric line, absent in some fossil specimens (OH 20) but not in others (STS 14, SK 82, SK 97), is to some extent related to age and its expression even in adults of modern *Homo sapiens* is highly variable. Lovejoy and Heiple (1972) also refute the contentions that the posteriorly directed lesser trochanter falls outside the range of modern human variation, or that the greater trochanters of the Olduvai and Swartkrans specimens are relatively smaller than those of modern man. They assert that the more laterally placed shaft results in a merging of the greater trochanter into the proximal mass of the femur itself. They warn that what at first appears to be significant differences often turn out not to be significant when the total range of variation is known. In certain respects other femora specimens resemble the genus *Homo*. East Rudolf #736 and #999 show medially placed lesser trochanters, gradually widening shaft contours and anterior convexities which are more reminiscent of the modern hominid condition, and thus differ from the robust australopithecine pattern.

Two distal femora from Sterkfontein (STS 34 and TM 1315) show prominence of the lateral condyle in the region of the patellar groove. This is part of the mechanism in bipeds which counters lateral dislocation of the kneecap in full extension of the knee. Additionally, Day (1973: 37) describes the presence of asymmetrical grooves for the menisci on the flattened condylar surfaces as part of the knee-locking mechanism and the presence of grooving for the popliteal tendon in full flexion as part of the knee unlocking mechanism similar to that in modern hominids.

However, Preuschaft (1971), based on an analysis of postcranial specimens from Olduvai, believes that the specialized human knee joint is absent. The post cranial features show that the tibia was slender and the fibula stout and that the relative width of the medial femoral condyle in comparison to the lateral and the contour of the patellar joint surface of the femur differ from the modern human condition. Preuschaft finds that the patellar joint is not elevated, in which case the patella could slip laterally on contraction of the quadriceps muscle. This is unlike the condition found in modern forms, where the patella is prevented lateral movement by an elevated joint. The Olduvai tibia and fibula shafts (OH 35) are described by Davis (1964: 967-968) and are essentially hominid in form except for certain specific characteristics. The shafts exhibit a more rounded anterior border similar to that in the pongidae associated with an extension of Tibialis anterior on the antero-medial surface of the bone in contrast to the sharp border seen in modern forms. Midshaft, the tibia shows greater extension for Tibialis posterior than for Flexor digitorum longus, again in contrast to *Homo sapiens*. Davis believes that the adaptations to bipedalism were more evident in the ankle but perhaps less well developed at the knee joint and that the upper tibia end appears to be intermediate between apes and man in the marking for Popliteus and the extent of attachment of Soleus onto the tibia.

Day (1976a) believes this to be in error due to what he feels is a misidentification of the soleal line. He claims this line is actually located in the upper end of the posterior aspect of the tibia which is next to the missing area which would show the attachment of Popliteus. The Olduvai specimens show many similarities to the KNM-ER 1500 tibia ascribed to *A. boisei*.

On the other hand Day (1973: 42), in his description of the KNM-ER 803 tibia demonstrates several differences from the Olduvai specimen and KNM-ER 1500. He describes the shaft as being relatively straight with a rounded anterior border which displays a strong area of attachment for the Soleus muscle similar to the modern condition. The posterior border is also rounded and separates the medial and postero-lateral surfaces. It is interrupted by a heavy oblique line that demarcates the popliteal surface above. From the outer margin of this line a well marked "vertical line" runs inferiorly separating the attachment areas of Flexor digitorum longus and Tibialis posterior.

Preuschaft (1971: 238) suggests that the anteriorly tilted position of the distal tibial joint surface on the Olduvai specimen indicates a much more displaced center of gravity to the rear of the body. The shaft of the Olduvai fibula on the other hand is nearly identical to that of modern man in that the apparent musculature is consistent with powerful plantar flexion of the foot (Davis 1964: 967).

The most complete foot bones are those of OH 8 which again show principal affinities with those of Homo sapiens. This specimen consists of twelve separate bones found in close association at the floor of site FLK NNI. They articulate to form a small left tarsus and metatarsus. Described by Day and Napier (1964), Day (1967), and Day and Wood (1968), the presence of an articular facet between the bases of the first and second metatarsals demonstrates the absence of an opposable toe (Preuschaft 1971). Lewis (1972), on the other hand, claims that a locking mechanism at the hallucial tarso-metatarsal joint is present. This particular form of joint is one primarily seen in arboreal primates and evolved as a means of stabilizing a grasping or opposable hallux. In addition to this primitive feature, the tilt of the talus, width of the horizontal talar neck angle, and the pattern of metatarsal robusticity (metatarsal 1 >5 >3 >4 >2 as opposed to the most common pattern found in Homo sapiens, 1 >5 >4 >3 >2) may also indicate that the striding gait of Homo sapiens had not yet been achieved. In opposition to this idea, Archibald, Lovejoy and Heiple (1972) find the metatarsal pattern fully commensurate with a striding bipedal gait: in many populations of modern forms substantial variability in relative robusticity exists, and this variability appears to have no significance in terms of gait pattern. Those pertinent features indicative of a striding gait are the very robust M-5 and the relatively reduced M-2. Additional details are provided for talus morphology from specimen KNM-ER 1476a whose features resemble that of the Olduvai talus. Morphological similarities are seen in the medially placed dorsai trochlear groove, the common-shaped tibial facet with dorsiflexion "stop" mechanism, a wide, horizontal angle of the neck, a similarly placed head on top of the neck, and trochlear radii that are equal (indicating a stationary axis of the ankle joint). Day (1976a) feels that most of the postcranial material from Olduvai are much more similar to that ascribed to Australopithecus rather than to Homo and this may account for those differences seen in material from localities in the East Rudolf area.

For example, recently Wood (1974) showed in a canonical analyis study of the right talus (KNM-ER 813a) from East Rudolf, attributed to the genus Homo, that in this instance the locomotor pattern indicated was clearly that of modern Homo sapiens. The low horizontal angle and the high torsion angle of the neck are both features of a non-prehensile propulsive bipedal foot. Day (1973: 42) also notes that the third left metatarsal from KNM-ER 803, ascribed to the genus Homo, is sufficiently developed dorsoventrally to withstand propulsive forces and is curved in torsion consistent with the formation of a transverse tarsal arch. The differences found in these two tali from those described for OH 8 may have phylogenetic significance, especially in view of the fact that Lisowski, Albrecht and Oxnard (1974) have shown that the morphological resemblance between the tali from Kromdraai and that from Olduvai is more clearly aligned to that of the modern Orangutan than any other modern pongid or hominid group. Only one terminal phalanx of a robust australopithecine from Kromdraai (TM 1517k) shows similarities to the specimen from Olduvai (OH 10). In terms of the degree of shaft torsion, both fossils are clearly unlike that of any prehensile primate foot. These features show that whatever is the significance of the differences found in the australopithecine and Homo lower limb material, the locomotion of both groups of hominids was clearly bipedal of one type or another.

UPPER LIMBS

In the East Rudolf succession as in many other areas the lower limbs are better represented than the upper limbs and the skeleton of the trunk is virtually unknown. Although one scapular fragment is known from East Rudolf as well as one from Sterkfontein (STS 7) and the Hadar (AL 288 IL) almost nothing is known of how the upper limb attached to the trunk. Regardless of this Stern (1976) and Tuttle (1974) have reviewed the evidence from comparative anatomy of living and fossil primates and have concluded that there is abundant evidence for a brachiating (=antipronograde) arboreal common ancestral stage in the hominoid lineage, and concluded that at least in the earlier hominid groups arborealism played a much greater role in locomotor activity than has been currently suspected.

The single clavicle fragment from Olduvai has been described by Napier (1965) who claimed that the clavicle had few distinguishable differences from those of modern Homo sapiens. The clavicle showed a smooth posterior-inferior groove indicating a steep thoracic inlet which led to the view that movements at the shoulder girdle were approximately the same as in moderns. This position was criticized by Oxnard (1968) who examined the extent of clavicular torsion and suggested that it was structurally modified toward suspensory locomotion. In addition the medial end of the fragment is slightly modified to suggest that the scapulae were set relatively higher than in modern man. Day (1967a), however, countered that the angle of clavicular torsion is not possible to construct with accuracy because both ends of the bone are missing and the bone is itself internally cracked. Additional anatomical comparisons with both modern apes and humans could not separate the bone from the modern human group except to suggest maleness rather than femaleness. In regards to the scapula, Stern (1976) observes a similarity between two measurements (axillo-glenoid angle and the axillo-spinal angle) taken from the Sterkfontein scapular fragment and the same two measurements taken from the scapula of gibbon. These angles appear to reflect the cranial orientation of the glenoid cavity and the rotatory abilities of the Scapulothoracic muscles. Stern believes that this indicates use of the upper limb above the head as an important component of positional behavior.

Little evidence exists as to the proportion of upper limb length to lower limb length (see Afar hominids). The incomplete humerus STS 7 is a robust and relatively long bone, and the suggestion has been made that the upper limb was slightly longer in proportion to the lower limb than is the case in modern man. The South African post cranial material, however, is not articulated except perhaps for TM 1517 from Kromdraii and it is impossible to determine if one limb bone belongs to the same individual as another. McHenry (1974: 335), however, is of the opinion, based on the post crania of Kromdraai TM 1517, that the humerus is proportionately much longer than that of modern hominids.

Of the East African material six humeral fragments have been recovered from East Rudolf of which #739 is the most important. The shaft of this robust right humerus is medially curved and marked with prominent muscular impressions and a deep intertuburcular groove. The olecranon process is shallow and lacks the steep lateral wall typical of knucklewalkers. McHenry's (1973) study of the large Australopithecus humerus KNM-ER 739 demonstrated that it is functionally distinct from the humeri of living hominoids but he was unable to determine whether or not it was used in locomotion or solely for manipulation. Kay (1973), comparing locomotor function and body weight, concludes that the KNM-ER 739 humerus is of a size to be expected for a bipedal hominid. He proposes that the robust Australopithecus was a facultative rather than habitual biped. McHenry (1973b) believes, however, that Kay's estimation of body weight for this specimen is too low by some 80-100 lbs because the estimate was based on the South African robust forms which McHenry considers smaller than the hyper-robust forms of East

Africa. Using Kay's regression equation but substituting a greater body weight of 225-250 lbs, the KNM-ER humerus sould bear the same relationship to the regression line as does modern *Homo sapiens*.

Additional results on distal humeri (KNM-ER 739, Kanapoi, TM 1517) were given from clustering analysis performed by McHenry (1975) which grouped the Kanapoi humerus with *Homo*, the specimen from Kromdraai with *Pan*, and the specimen from East Rudolf in a unique cluster of its own but closer to *Gorilla*. The Kromdraai specimen is unique in having a high capitulum but unlike *Pongo* in all details. This specimen is unique in that it lacks a lateral trochlear ridge, which has been present in all pongid studies. According to McHenry (1975), these characteristics do not yield themselves to functional explanation because the two closest related ape forms, *Pongo* and *Gorilla*, locomote in different ways. The Kanapoi fossil, dated at approximately 4.0 m.y. shows the early emergence of a *Homo*-like elbow. McHenry (1975: 240) concludes that all three fossils may belong to separate taxa.

Further evidence of forelimb morphology was discovered by Eck in 1970 from the Shungura Formation in the lower Omo basin. The specimen, described by Howell and Wood (1974) and McHenry, Corruccini and Howell (1976) was a nearly complete ulna of a robust australopithecine whose morphology shows marked structural differences from modern *Homo*. The ulna is posteriorly convexly curved rather than sinuously curved (seen from below) as in the modern forms. This morphology is similar to that seen in living knucklewalkers. The interosseous border forms an irregular crest unlike the accentuated crest of modern ulnae, indicating perhaps significantly different patterns of stress placed on the bone. The proximal end of the anterior surface is separated by an irregular ridge of bone from the triangular-shaped area just distal to the radial notch. In contrast to prominent hollowing for the radial tuberosity in modern hominids, this rough-surfaced area is only slightly hollowed. Additionally, the length of the shaft suggest elongation of the forelimb for this specimen. This combination of features is indicative of some morphological adaptations not unlike those seen in modern knucklewalkers. Additional ulnae in the sample are two proximal fragments (TM 1517 and KNM-ER 1500) and another (OH 3), lacking its distal portion, which shows greater curvature than the Omo specimen.

In 1962 Napier described "21 hand bones" from site FLK NNI Olduvai Gorge. In a recent revision Day (1976a) claims that of these 21 bones, 6 are not hominid and one appears to be an unidentifiable vertebral fragment. Of the remaining 15, 7 belong to a juvenile individual, 6 are questionable as to age and 2 belong to an adult. Those of unknown age consist of a right trapezium and scaphoid, a left capitate, 2 distal fragments of proximal phalanges and the base of a second metacarpal. Those belonging to the juvenile consist of 1 terminal thumb phalanx, 2 terminal finger phalanges and 4 middle right phalanges II - V. These juvenile bones are clearly hominid and suggest a hand capable of powerful finger flexion with the possession of an opposable thumb. The adult phalanges noted by Oxnard (1972) are highly curved with disproportionately small heads and deeply guttered ventral sides with prominent lateral and medial ridges for the attachment of the flexor sheaths; all of which are suggestive of the hanging-climbing form of locomotion seen in Colobus. Day suggests that these adult phalanges may have belonged to the extinct giant Paracolobus chemeroni. Additional available hand material is limited. The two proximal phalanges (KNM-ER 164) reported from East Rudolf are described as very modern and similar to Homo sapiens.

An increasing amount of evidence is suggestive that the morphology of the robust australopithecines differed significantly from that of Homo. The relative elongation and presence of specific morphological differences imply the possibility that the body of the robust forms was supported by the forelimbs, either in suspensory postures as proposed by Robinson (1972) or in terrestrial knucklewalking as proposed by Leakey (1971: 231, 241). The morphological pattern, however, is still too insufficiently defined to argue for any specific form of locomotion.

INTERPRETATIONS

Although precise reconstruction of the gait and stance of the earlier hominid forms is difficult, it can be assumed that it was probably not identical to the modern form. The same broad anatomical pattern, as mentioned before, is obvious. Some anatomists, such as Day (1973), are cautious in their evaluations of the anatomical differences, stating that at this stage of our knowledge we do not completely understand what these differences in morphology mean in terms of locomotor function. Others such as Lovejoy (1972) and Robinson (1972), interpret these differences in terms of more specific behavioral patterns.

The study of the post crania has been hampered by poorly preserved remains and inadequately reconstructed specimens. Day (1973: 30) believes that the most complete pelvic remains from Sterkfontein (STS 14) contain major anatomical errors in reconstruction. Yet, evidence (Day 1973: 42) from the available East African post cranial bones (KNM-ER 803, 737) indicate clearly a bipedal gait.

According to Robinson (1972: 240-242), the capacity to stride is a complex capacity with many contributing components; the effective control of lateral balance and the extension of the femur being two of the most important considerations. The major difference between pongid and hominid bipedal walking concerns the orientation of the ischial shaft which, in the bipedal pongid, becomes parallel to the femoral shaft and thus limits the power of the extensors of the thigh to produce a striding gait; therefore, only short steps are possible. In hominids the reorientation of the ischial shaft is directed backward and downward, in a position such that the hamstrings can operate to extend the thigh past the vertical position. According to Robinson, the gracile australopithecine had a sufficiently well developed lumbar curvature to indicate a similar relationship with the innominate as in the modern hominid forms; consequently, he proposed that this aspect of a striding gait was fully developed. Robinson concludes, however, that the robust condition was a compromise between the quadrupedal arboreal climbing pattern of the African apes and efficient bipedalism, implying a combined bipedality with some locomotor activity that required power in the use of the limb extension mechanism.

The length of the ischium has also been used to demonstrate differences between Australopithecus and modern forms. Robinson (1972: 243) claims, however, that the gracile forms had clearly shorter ischia than even the average found in modern man. Due to the relatively small size of the ischial tuberosity, the hamstrings could not have been as large or as powerful as in the pongidae, and thus the extensor complex of the thigh was specialized for speed and for an increase in length of step, perhaps even greater than in modern man.

Lovejoy (1973) provides additional information based on STS 14 which supports Robinson's diagnosis of gait of the gracile australopithecine. He outlines three principal components of a bipedal gait: 1) trunk progression and maintaining momentum, 2) trunk support and the abductor mechanism, and 3) limb progression and the pendulum gait. In each category, he claims, the joints and muscles involved were sufficiently adapted to perform in bipedal striding.

Lovejoy (1973: 157) has claimed that in some respects these morphological features seen in the australopithecines are indicative of more efficient bipedal locomotion. In this regard, the index of width to height of the ilium given at 134, due to the anterior extension of the ilium into a beak configuration in the Swartkrans fossil and noted as considerably above the modern mean of 119, is meaningful only in terms of the efficiency of the hip abductor mechanism. The lateral iliac flare and anterior iliac extension places the origin of the abductors more lateral to the acetabulum; the longer femoral neck places the insertion more lateral to the hip joint, and provides a longer power arm for the abductor muscles. This implies that less abductor force is necessary to stabilize the hip in side to side swaying and in controlling pelvic tilt, resulting in less stress being placed on the femoral head and acetabulum. Certainly the size of the individual is an important consideration (SK 3155 is estimated to have weighed about 70 lbs.) and the consequent torque developed at the hip joint during a one-legged stance would be small if compared to the heavier later hominid forms. He further claims that the change in the hip abductor mechanism is from one of greater efficiency to one of lesser efficiency and is the result of selection over time on the female pelvis to maintain adequate pelvic dimensions for the enlargement of the fetal cranium.

Evidence for robust australopithecine locomotion is less complete. No direct evidence exists for the presence of the lumbar curve; there are no known sacra. Original opinions on the gait were based primarily on the distorted SK 50 right innominate and ranged from a waddling and shuffling form of bipedalism (Napier 1964), to tree-climbing and inefficient bipedalism (Robinson 1972), to essentially modern bipedalism (Lovejoy et al 1973). Though a new right pelvic fragment from Swartkrans (SK 3155) from the pink breccia lacks the ischium and pubis most of the ilium is complete, lacking only bits of the crest and the anterior-superior iliac spine. It is not as distorted in shape as the earlier discovered SK 50 fossil. Hominid traits of the pelvis are obvious: the iliac blade is low, broad and thick in the region for the attachment of Gluteus minimus and medius and there is a well developed sciatic notch. The anterior-inferior iliac spine is present and well developed, as well as the groove for the iliopsoas muscle tendon. An oblique angle can be seen between the iliac blade and the acetabulum. Comparisons of the STS 14 and the SK 3155 do show certain differences. The relationship between the width of the ilium and size of the acetabulum is different in the two forms. The sacral articular surface of STS 14 is relatively smaller than that of SK 3155, and there are certain differences in the ischia, primarily the extended length in the robust form. However, this would not modify the limb extensor mechanism to any significant degree towards that found in the pongidae. Resemblances of this new specimen to other australopithecine pelvic bones both robust and gracile is apparent, and these similarities suggest that the pattern of their gait was similar and the differences were probably not fundamental to bipedalism. It must be noted that, in this respect, the evidence from the pelvis echoes that from the other lower limb fossil material.

CATALOGUE OF FOSSIL HOMINID POST CRANIA

	SPECIMEN #	SITE LOCATION	DESCRIPTION
HAND	18-1848 (1970)	Loc Omo 18	left middle phalanx
	OH 7	FLK NNI Olduvai	9 phalanx 1 meta carpal, and 3 carpals of a juvenile
	OH 18	FLK Olduvai	phalanx
	KNM ER 164	Ileret Area 104	right (?) Three Phalanges, Metacarpal
	TM 1526	Sterkfontein lower breccia	capitate
	AL 288-1W	Al 288	left capitate
	TM 1517	Kromdraai	left metacarpal II
	TM 1517	Kromdraai	proximal phalanx
	AL 288-1X,Z	AL 288	phalanges
Radius	75-S-1 317 (1970)	Loc Omo 75-S	proximal end
	KNM ER 3736	Area 105 upper KF	proximal 2/3s
	OH 49	FLKNN	shaft
	KNM ER 1500	Area 131	proximal end
	MLD 15	Makapansgat	right distal end
	MLD 16	Makapansgat	right proximal end
	MLD 32	Makapansgat	left prximal end
	STS 68	Sterkfontein lower breccia	proximal end
	Al 288-1V	AL 288	left distal end
	SK 18	Swartkrans pink breccia	proximal end
	AL 288-1P	AL 288	right proximal end
	AL 288-1Q	AL 288	right distal end

	SPECIMEN #	SITE LOCATION	DESCRIPTION
ULNA	40-19	Loc 40 (Omo)	right ulna
	TM 1517	Kromdraai	right proximal end
	KNM ER 803	Ileret	fragment
	AL 288-1u	AL 288	left distal end
	KNM ER 1500	Area 131	proximal fragment and fragment of shaft
	AL 288-1T	AL 288	left proximal end
	OH 36	SC	complete except for distal end
	AL 288-1N	AL 288	right proximal end right distal end
HUMERUS	OH 13	MNK II (Olduvai)	distal humeral shaft
	KNM ER 1500	Area 131	fragments of shaft
	KNM ER 739	Ileret	right distal end and shaft
	AL 288-1R	AL 288	left proximal end
	AL 288-1S	AL 288	left distal end
	KNM ER 1504	Koobi Fora	right distal end
	KNM ER 1473	Area 131	right proximal fragment
	KNM ER 1591	Area 12	complete but lacking head
	KNM ER 740	Ileret	left fragment of distal end
	KNM ER 3735	Area 116 Lower KF	weathered distal right end
	Kanapoi Hominid 1		left distal end
	KNM ER 1591	Ileret	lacking proximal end
	MLD 14	Makapansgat	distal right fragment of shaft
	MLD 39	Makapansgat	right distal fragment
	STS 7	Sterkfontein	proximal fragments
	STS 50	Sterkfontein	right distal end
	SK 860	Swartkrans	distal end

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	SPECIMEN #	SITE LOCATION	DESCRIPTION
HUMERUS	TM 1517	Kromdraai	right distal end
	AL-288-1M	AL 288	right nearly complete
SCAPULA	STS 7	Sterkfontein Lower Breccia	fragmentary
	KNM ER 1500	Area 131	fragmentary
	AL-288-1L	AL 288	right glenoid cavity
CLAVICLE	OH 48	FLKNN I	complete clavicle
	MLD 20	Makapansgat	right acromial extremity
	MLD 36	Makapansgat	left acromial extremity
RIBS	OH 50	FLK NN (Olduvai)	rib shaft
	AL 288-AU A2	AL 288	rib fragments
VERTEBRA	105-7	Loc 105 (Omo)	lumbar
	KNM ER 164	Area 104	seventh cervical, first thoracic
	STS 14	Sterkfontein Lower Breccia	9 thoracic, all lumbar, sacrum
	STS 65	Sterkfontein Lower Breccia	vertebral centrum
	SE 2398	Sterkfontein Middle Breccia	vertebrae
	SK 853	Swartkrans	lumbar vertebrae
	SK 854	Swartkrans	axis
	SK 3981a	Swartkrans	last thoracic
	SK 3981b	Swartkrans	last lumbar
	AL 288-1AA	AL 288	lumbar
	AL 288-AC → AM	AL 288	thoraic and fragments
PELVIS	SK 3155b	Swartkrans	adolescent nearly complete ilium, parts of ischium, pubis
	AL 288-1AO	AL 288	left ilium
	SK 1590d	Swartkrans	innominate parts

	SPECIMEN #	SITE LOCATION	DESCRIPTION
PELVIS	MLD 7	Makapansgat	left adolescent ilium
	MLD 8	Makapansgat	right adolescent ischium
	MLD 25	Makapansgat	left adolescent ilium
	MLD 21	Makapansgat	fragmentary ilium
	MLD 35	Makapansgat	fragmentary infant ilium
	STS 14	Sterfontien Lower Breccia	left and right innominates
	STS 65	Sterkfontein Lower Breccia	1/10 pubic fragment
	SK 50	Swartkrans	right innominate lacking iliac crest
	KNM ER 3228	Lower Member KF	right innominate lacking pubic and ischial rami.
	TM 1605	Kromdraai	ilium lacking iliac crest
SACRUM	AL 288-1AN	AL 288	complete
FEMUR	754-8	Loc 754 (Omo)	portion femoral diaphysis
	OH 20	HWK II (Olduvai)	left proximal shaft and neck
	KNM ER 736	Koobi Fora	left femoral shaft
	KNM ER 738	Koobi Fora	left shaft and proximal end
	KNM ER 737	Koobi Fora	left femoral shaft
	KNM ER 999	Ileret	left femur lacking lateral condyle
	KNM ER 815	Ileret	left femur without head
	KNM ER 993	Ileret	right femur
	KNM ER 1463	Area IA Ileret	right diaphysis
	KNM ER 1481	Karari Escarpment Area 131	left femur
	KNM ER 1465	Ileret Area 8	left proximal fragment
	KNM ER 1472	Karari Escarpment Area 131	right femur

	SPECIMEN #	SITE LOCATION	DESCRIPTION
FEMUR	KNM ER 1503	Ileret Area 127	proximal right end
	KNM ER 1475	Karari Escarpment Area 131	right proximal end and shaft
	KNM ER 1592	Ileret Area 12	distal half
	AL 288-1AP	AL 288	left femur
	KNM ER 1505	Koobi Fora Area 123	left proximal and shaft fragment
	KNM ER 1500	Koobi Fora Area 131	right proximal and distal portions
	KNM ER 1807	Area 103	right shaft
	KNM ER 3730	Area 102 (?) Upper KF	weathered distal end
	KNM ER 1809	Area 127	right shaft
	KNM ER 3728	Area 100 Lower Member	left femur shaft and neck
	AL-129-3	Loc AL 129 (Afar)	right proximal end
	AL-288-1	Loc AL 288	diaphysis fragment
	AL[illegible]128-1	Loc AL 128	proximal left end
	[illegible]288-1	Loc AL 288	right diaphysis
	AL-129-1	Loc AL 129	distal right end
	AL-211-1	Loc AL 211	right proximal fragment
	MLD 17	Makapansgat	femoral head
	TM 1513	Kromdraai	left distal end
	STS 14	Sterkfontein Lower Breccia	proximal end
	STS 34	Sterkfontein Lower Breccia	right distal end
	STS 65	Sterkfontein Lower Breccia	left proximal femur
	SK 82	Swartkrans	right proximal femur
	SK 97	Swartkrans	right proximal femur
	SK 1590d	Swartkrans	head of proximal end

	SPECIMEN #	SITE LOCATION	DESCRIPTION
FEMUR	TM 3601	Kromdraai	distal end femoral condyle
	KNM ER 803	Lake Rudolf	left shaft
TIBIA	OH 35	FLK	left shaft and distal end
	KNM ER 741	Ileret	left proximal end and shaft
	KNM ER 1500	Koobi Fora Area 131	left distal end and fragments of shaft
	KNM ER 813	Koobi Fora	fragmentary tibia
	KNM ER 1471	Koobi Fora Area 131	proximal right half
	KNM ER 1481	Karari Escarpment Area 131	distal end
	KNM ER 1476	Koobi Fora Area 105	left proximal and fragmentary shaft
	KNM ER 1810	Area 123	left proximal portion
	KNM ER 2594	Ileret Area 6A	proximal fragment and fragmen of shaft
	AL-129-2	AL 129 (Afar)	right proximal
	KNM ER 2596	Ileret Area 15	distal fragment
	KNM ER 803	Ileret	left shaft
	AL 288-IAQ	AL 288	proximal right end
	AL 288- IAR	AL 288	distal right end
FIBULA	KNM ER 1481	Karari Escarpment Area 131	distal portion
	KNM ER 803	Ileret	fragment of shaft and distal end
	KNM ER 1500	Koobi Fora Area 131	right distal portion
	AL 288-IAT	AL 288	right distal end
	OH 35	FLK Olduvai	left distal end and shaft

	SPECIMEN #	SITE LOCATION	DESCRIPTION
FOOT	576-18	Loc 576 (Omo)	right? distal phalanx hallux
	OH 8	FLK NN I (Olduvai)	left 7 tarsals, 5 metatarsals
	KNM ER 997	Koobi Fora	proximal metatarsal
	KNM ER 813a	Koobi Fora	right talus
	KNM ER 1464	Ileret Area 6	right talus
	KNM ER 1815	Ileret	right talus
	KNM ER 1476	Koobi Fora Area 105	left talus
	TM 1517	Kromdraai	right talus, proximal and distal phalanx
	OH 43	Olduvai	matatarsals
	KNM ER 803	Ileret	talus, third left metatarsal phalanges
	AL 299-IAS	AL 288	right astragulus

The following specimens are composed of associated remains each belonging to a single individual.

KNM ER 1500	Koobi Fora Area 131	∼ 2.0 m.y.
KNM ER 803	Ileret Area 8A	∼ 1.5 m.y.
AL 288	Hadar	> 3.0 m.y.
STS 14	Type site Sterkfontein	∼ 2.0 m.y.

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ENDOCRANIAL VOLUME IN PLIO/PLEISTOCENE HOMINIDAE

Endocranial volume of fossil hominids has been used by many workers to demonstrate whether or not a particular speciemn has reached a specific level of development. The fact that natural selection kept favoring larger brains throughtout the Pleistocene has been well demonstrated. Yet as Holloway (1966: 115) suggests, there has been no firm connection made between the neural structures of the cortex and the increasing behavioral complexity upon which natural selection was operating. In other words, endocranial volume which increased during the Pleistocene period has not been related to absolute or relative differences in cultural capabilities. The same is true for modern Homo sapien which has a range of nearly 1000 cc without measurable behavioral differences between the extremes of that range (Van Valen 1974).
Holloway suggests that other parameters, besides absolute volume, must be used to explain the increase in cranial capacity in the course of hominid evolution. According to Holloway (1966: 117), however, neural organization during the australopithecine stage resulted in a shift into essentially human behavior and the continuing changes resulted in greater degrees of behavioral complexities rather than kinds.

Attempting to understand hominid evolution through the study of increased cranial capacity is grossly oversimplifying the problem. Yet, Jerison (1963) has shown that though certain limitations on understanding exists in the study of fossil endocasts, specific information not only as to (1) total volume, but also (2) linear measurements producing indices of size, (3) proportional measures of surface areas, and (4) the diameters of nerve bundles as estimated from the cranial foramina can be obtained. Despite the valid criticisms most judgments concerning the evolution of the human brain use brain volume as the main quantitative basis, and Jerison (1963: 268) points out that large random errors approaching 20 percent exist in volume measures because only rarely is a natural endocast recovered from a deposit in perfect condition.

Earliest estimates (Broom and Robinson , 1948, Ashton, 1951) of existing fossil hominids yielded figures of 415 cc (STS 5), 450 cc (TM 1511), and 650 cc (TM 1517, the type specimen *Parathropus robustus* from Kromdraai). It was believed that the males had substantially larger brains than the females based on the single large mandible (STS 8) which Broom and Robinson estimated must have supported a skull with an endocranial volume of "well over 700 cc and perhaps more than 750 cc." Since the primary purpose of these early works was to demonstrate the human qualities of the fossil forms, Broom and Robinson proposed that "if *Pleasianthropus* was not quite human, it was nearly human."

By the 1960's the idea of the cerebral "rubicon" of brain size differentiating man and apes formulated by Keith, Vallois and others, was replaced by the knowledge previously stated that brain volume has little relationship to functional behavioral capabilities. Because of interest in cranial capacities from the point of view of determining where the australopithecines fit in relation to other huminoids, Tobias (1963, 1971) reviewed the estimates for cranial capacity in the known australopithecine and modern hominoid forms. Until the discovery of the OH 5, it had generally been considered that the robust australopithecines had larger brains than the gracile forms, and estimates of cranial capacity varied between 650 cc and 1000 cc. The well-preserved skull OH 5 type specimen of Zinjanthropus boisei was the first of the robust australopithecines to enable an accurage assesment of cranial capacity. Tobias (1971) gives an estimate for this specimen at 530 cc, and in addition for SK 1585, at 500 cc. Holloway's (1970, 1972) estimate for the same specimen

(SK 1585) is 530 cc. More recently, Holloway (1973) has calculated the endocranial volume of two robust specimens from East Lake Rudolf, KNM-ER 406 and 732, which yielded figures of 510 and 506 cc, respectively.

For the gracile australopithecine Tobias (1971) reports on Taung (540 cc), STS 60 (435 cc), STS 5 (480 cc), STS 71 (480-520 cc) STS 19/58 (530 cc) and MLD 37/38 (480 cc) and established a mean endocranial volume at 494 cc, and a total range for adult australopithecines including the two robust forms, between 435-540 cc. Though this compares with a similar estimate by Holloway (1970) of the australopithecine range between 428-530 cc, this differs from estimates given by Wolpoff (1969) of a mean value of 521 cc and a range between 435-657 cc which includes Olduvai Hominid 7. Tobias (1971: 27) demonstrates that an estimate can be made of the projected australopithecine population range based on the sample mean ± 3 standard deviations which gives the values of 370-618 cc. The estimated population range is consistent with that reported by Zuckerman (1928) for chimpanzees (290-500 cc) and by Schultz (1965) for pygmy chimpanzees (275-380cc). However, it is not consistent with estimates of 1000 cc for the maximum limits of the australopithecine cranial capacity (Broom and Robinson 1952, Dart 1956).

Endocranial volume enters into the issue of the status of many individual fossils, the most notable being Olduvai Hominid 7 designated the type specimen of Homo habilis Leakey. Tobias (1964, 1965) estimated the range of possible values for this juvenile specimen which varied from 643-724 cc, with a mean of 680 cc which exceeds the mean for the australopithecines by slightly more than 3 standard deviations (Tobias 1965, 1968). Tobias' estimate of the mean of OH 7 was confirmed by Holloway (1965) but revised by Tobias (1968) to 657 cc. The question of whether or not this difference was of taxonomic significance was argued by Holloway and Tobias (1966): Tobias claiming that our knowledge of australopithecine variability was insufficient to suggest whether or not these hominids were highly variable in cranial capacity comparable to Gorilla with a high coefficient of variability (13.6) or comparable to Pan with a low coefficient of variation (6.8). Wolpoff (1969, 1970), however, claims that his estimate of the australopithecine mean (521 cc) justifies the inclusion of OH 7 within his taxon Homo africanus. Pilbeam (1969, 1970) criticizes this methodology and claims that Wolpoff's "Sample" is not drawn from a single population in time or space, and, therefore, it is unwise to draw any taxonomic conclusions.

Based on his more recent australopithecine estimates, which give a mean of 464 cc (including two robust forms OH 5 and SK 1585) Holloway (1970a, 1970b) argues that it is highly unlikely that the robust and gracile forms were male and female of the same species and disagrees with Wolpoff (1969) that OH 7 should be included taxonomically with the australopithecines from South Africa. Similar arguments were proposed for the inclusion of OH 13 and 24 within the genus Homo rather than Australopithecus (Tobias 1972, Holloway, 1973), whose estimates of cranial capacity approached 650 cc and 590 cc, respectively.

The question of the affinities of the Taung skull has remained open because of the young age of this specimen and the difficulty in estimating what additional development this individual would have made if it had lived to reach adulthood. Ashton and Spence (1958), by determining the dental age of the Taung child, determined that the cranial capacity had reached 90 to 94 percent of its adult values; thereby establishing the "adult value" at 562 cc replacing earlier estimates of 600 cc. More recent reconstructions of the Taung endocast (Holloway, 1970) produced significantly different results which averaged 440 cc. If the Taung child is indeed a late robust australopithecine, the estimate for endocranial volume is considerably lower than those of adult individuals of the same period.

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E. PROBLEMS IN INTERPRETATION:

The Taxonomy of the Early Hominidae

TAXONOMY OF THE FOSSIL HOMINIDS
South Africa

The result of paleontological explorations in South Africa brought to light at least two distinct forms of fossil hominid recognized in the faunal remains. Robinson (1954, 1963) established generic distinctions between two of the forms of hominids commonly known as the gracile and robust form of Australopithecine. Taxonomic distinctiveness was supported on the one hand by morphological differences between the two fossil forms and on the other hand by ecological differences which were based primarily on diet. Brain's (1958) original work on the climatic sequence of the South African cave sites suggested that fossiliferous material of robust australopithecines was accumulated in caves during wetter periods of heavier rainfall, and that the caves associated with the gracile forms were filled during periods of less rainfall. The diet of the robust form was proposed to be primarily vegetarian. Brain's work was criticized by Vrba (1975) whose investigations suggested a drier period for the accumulation of the deposits of the robust australopithecine bearing caves. Thus, the argument is whether the robust forms were eating vegetable matter in a wetter and more luxuriant environment, or one of drier conditions. If the latter case is proved to be a more reasonable reconstruction of the paleoenvironment, Jolly's (1970) argument for "small object" feeding on tough grassland vegetable material may be pertinent to our understanding of the persistence of the robust form for a duration of over a million years.

The morphological differences in the two forms are primarily found in the dentition and skull. According to Robinson (1963), the morphology of the first lower deciduous molar (dm$_1$), the shape of the permanent lower canine, the proportion of the anterior and posterior teeth, shape of the palate, the shape and structure of the face and of the braincase are sufficient diagnostic characters to justify separation of the two hominids into two distinct genera: *Paranthropus* which is represented at Swartkrans and Kromdraai, and *Australopithecus*, which is represented at Sterkfontein (=*Plesianthropus*) and Makapansgat. Robinson retained the subfamilial rank, Australopithecinae, to accommodate these two genera. Dart, however since 1948, has held the view that the whole australopithecine group represented a single genus with two species within the family Hominidae. This view has been supported by Washburn and Patterson (1951), Oakley (1954, 1956), LeGros Clark (1964, 1967) and Leakey, Tobias and Napier (1964). Tobias (1968) proposed that three species be recognized under the single genus, namely *A. africanus*, *A. robustus* and *A. boisei* (OH 5) and provided diagnosis for each.

Recent attempts to sink the genus *Australopithecus* had their origins with Mayr ('50) who proposed a classification of the australopithecines as distinct species of the genus *Homo*, specifically *Homo transvaalensis*. He subsequently abondoned this view ('63).

The arguments for a single hominid genus leading to modern man was revived form two points of view. On is by Robinson (1972: 1-11), who includes the genus *Australopithecus* (but not *Paranthropus*) in the same phyletic line as *Homo*. He claims that because *Australopithecus* represents an early phase in the establishment of the adaptive pattern characteristic of modern man that it would be logical to sink the *Australopithecus* into the genus *Homo* as a junior synonym. Thus, his most recent classification of known Plio-Pleistocene hominids includes only two genera *Paranthropus* and *Homo*. After lengthy justification, Robinson concludes that the appropriate specific name for those specimens of the gracile australopithecine group is *Homo africanus*.

The second point of view was first proposed by Wolpoff (1968, 1971) whose extreme lumping of both the robust and gracile australopithecines into a single species has not met with general acceptance. The basis for the single species hypothesis is the nature of the primary hominid adaptation which Wolpoff claims is culture or structured learned behavior. Wolfoff (1971: 607) argues that in order for closely related species to coexist sympatrically "they must differ from each other in such a manner that they do not enter into a 'struggle for existence' in which one succeeds at the expense of the other." He concludes that for culture-bearing hominids this would be a particularly difficult thing to avoid. Wolpoff (1973) redefends his position claiming that the criteria which are used to separate the South African australopithecines into two taxa are either unverifiable or related only to general body size differences. Recently Wolpoff and Lovejoy (1975) rediagnosed the genus *Australopithecus* with the single species *africanus*, and incorporated as junior synonymns all members of the taxons *Paranthropus*, *Paraustralopithecus*, *Plesianthropus*, *Zinjanthropus*, *Meganthropus africanus*, *Homo habilis* and *Telanthropus*. These authors suggest that the taxon *Australopithecus* should be retained and not relegated to the genus *Homo*. Furthermore, they argue that the discovery of additional specimens occupying the same adaptive plateau as the known australopithecine will certainly increase the knowledge of the amount of morphological variability used to define the genus and thus approach the larger range of variation used to define the genus *Homo*.

The single species hypothesis has more recently been considered with regards to the hominid remains from the Koobi Fora Formation, Lake Turkana. Leakey and Walker (1976) present equivocal evidence for the occurence of *Homo erectus* and the large australopithecine. An adult cranium KNM-ER 3733 was found *in situ* in the upper member of the KF Formation. The cranium consists of a complete calvaria and much of the facial skeleton with several upper premolars and molars preserved. According to Leakey and Walker (1976) the cranium resembles that of *H. erectus* from Peking in morphological detail and endocranial volume.

In stratigraphically equivalent deposits within the upper member of the Koobi Fora Formation additional specimens of the robust australopithecines have been recovered *in situ*. One of the most complete skulls of this robust type of hominid is KNM-ER 406 which clearly demonstrates the contemporaneity of two hominid species. R. Leakey is inclined to treat the large australopithecine form as a subspecies of *A. robustus*, and claims that there is no convincing evidence for *Australopithecus* occurring earlier than examples of the *Homo* lineage.

The taxonomic position of the hominid specimens from Swartkrans originally described as *Telanthropus capensis* (Broom, 1950), has created a considerable debate. Consisting originally of a mandible (DK 15) and later a right mandibular fragment (SK 45), a maxillary fragment (SK 80) and finally a facial part of a cranium (SK 147), and an associated temporal fragment SK 8466 (the latter three belonging to the same individual, Clarke and Howell, 1972); it was first described as an early type of man morphologically distinct from the australopithecines. Dart (1955) believed it represented a female robust australopithecine. Pilbeam (1970) thought it was a gracile australopithecine, though he later (1972) revised this view. Howell (1967), on the other hand, was of the opinion that the specimens belonged to the taxon *Homo erectus*. This arguemnt followed Robinson's (1961) formal sinking of the genus *Telanthropus* into *Homo*, and Tobias and Von Keonigsvold's (1964) demonstration of the similarity of SK 15 with the *Homo erectus* mandible (Sangiran B) from Java, and Olduvai Hominid 13 (=*Homo habilis*). Wolpoff (1968, 1971) claimed however, that no morphological evidence validly distinguished these specimens from the other australopithecines. Conversely, he thought that "Telanthropus" represented an extension of the estimated australopithecine range of variation. This position was carefully reviewed and criticized by Clarke and Howell (1972) and Gutgesell (1970) who evaluated the diagnostic characteristics which were used to place the composite SK 847 within the genus *Homo*. Clarke and Howill (1972) refrained from placing the "Telanthropus" in the *Homo erectus* group because they suspected that the remains might prove to be conspecific with *Homo habilis* from Olduvai. The recent age determinations for the South African fossiliferous localities create certain new taxonomic problems. The placement of the Makapansgat deposit at the oldest end of the sequence appears, on the one hand, seems to be consistent with the evidence of the hominid fossils themselves. In Tobias' view (1973: 80-81) the Makapansgat hominids are characterized by traits which include some robust features in crania, jaws and teeth. Tobias (1969) speculated that perhaps more than one species of hominid was represented in the assemblage. Aguirre (1970) further claimed that the Makapansgat juvenile jaw, MLD 2, represented and adolescent *A. robustus*. More recently, Tobias (1973) revised his opinion and pointed out that in an early population of *A. africanus* which as close to the point of speciation into robust and gracile forms that intermediate characteristics might well be expected and that the speciemns from Makapansgat might be viewed as basal stem stock for later hominids.

The idea that *A. africanus* gave rise to two hominid lineages, one giving rise to the robust form and the other leading to the genus *Homo* has been criticized by Robinson (1972: 4-5) who suggested the possibility that the origin of the *Paranthropus* line extends back into the early Pliocene to fossils similar to those recovered by Simons and Chopra (1969) in India and attributable to the taxon *Gigantopithecus bilaspurensis*.

The recognition that the original australopithecine site at Taungs was much younger than previously believed also has had taxonomic implications. On the basis of these age estimates the Taung adolescent lived some 2 m.y. after those at Makapansgat or Sterkfontein. As for as the evidence presently shows, during the intervening time period, only early specimens of the genus *Homo* or *A. robustus* were present. In light of this, Tobias questions whether the Taung specimen in fact represents *A. africanus* as defined by the Sterkfontein and Makapansgat remains. Because of the small brain and dental characteristics it is excluded from the category *Homo erectus*. It may ultimately prove to be a late surviving member of *A. robustus* approximately contemporary with the East African forms from Chesowanja. According to Tobias (73: 82) if the Taung skull is removed as the type specimen of *A. africanus* under the rules of zoological nomenclature, it may be assigned a position of lectotype of *A. robustus*. However, arguments could be made, because of priority, to designate the Taung skull as the type specimen of *A. robustus*. If this occurred, the robust australopithecines would be placed in the taxon *A. africanus* which would make this taxon unavailable for use for the gracile form. This event would leave the question of what to call the gracile australopithecines open to further debate (see Olson, 1974).

EAST AFRICA

The discovery of Olduvai Hominid 5 from FLK I began an intensive search for early man in East Africa. The problems involving the taxonomy and relationships between the newly discovered fossils were fewer primarily because paleoanthropologists by this time had, for the most part, ceased regarding every new fossil hominid as a new species. Added to this was the trend in zoological nomenclature to expand the concept of variability in dealing with paleospecies which made it more likely that divergent specimens would be grouped within the same taxon.

The majority of problems in the literature arise in the description of fossil specimens from Olduvai Gorge. As early as 1959, Leakey described Olduvai Hominid 5 as a member of the sub-family Australcpithecinae which , in certain respects, recalled the genus Paranthropus, but he believed that the new specimen differed from both Australopithecus and Paranthropus more than those two genera differed from each other. As a consequence he created a new genus and species, Zinjanthropus boisei, and proposed a preliminary diagnosis (1959: 492-493) of the new taxon.

Robinson (1960) took issue with Leakey's description claiming that most of the differences Leakey proposed were the result of size. Zinjanthropus was somewhat larger and more muscular than the known South African forms. The other features of the new East African hominid, Robinson claimed, could also be demonstrated in the robust South African forms.

In 1961(a,b), Leakey announced the discovery of yet another specimen from the site of FLK NNI, a horizon claimed to be older than that of Zinjanthropus. This specimen OH 7 consisted of a nearly complete mandible associated with stone and bone tools. Leakey believed that it represented not an australopithecine but a primitive ancestor of the genus Homo. In 1964, Leakey, Tobias and Napier revised the diagnosis for the genus *Homo* and include a new species which they named *H. habilis*, the species name suggested by Raymond Dart. The type specimen of *Homo habilis* included the original mandible of OH 7 from Bed I. The paratypes included an incomplete cranium (OH 13) from MNK II, Bed II, associated post crania (OH 8) from FLK NNI, teeth and cranial fragments (OH 6) from FLK I, and a mandibular fragment (OH 4) from MNK I. Referred material included additional cranial fragments (OH 14) from MNK II, and a fragmentary skull with dentition (OH 16) from FLK II, Maiko Gully. Leakey subsequently placed OH 16 in the lineage leading to *Homo erectus* as represented by the skull from site LLK II. Mary Leakey (1969, 1971) provided additional referred material to *Homo habilis* including OH 24, a nearly complete cranium form Lower Bed I, site DK East, and OH 21, OH 27, isolated teeth from Bed I, FLK North and HWK East, respectively. M. Leakey (1971) (contra L. Leakey) includes OH 16 with the type specimen as part of the *habilis* group which represented males. Accounting for the differences by sexual dimorphism between these specimens and OH 13 and OH 24, M. Leakey refers to the latter specimens as females. The major importance of the discoveries at Olduvai was that it demonstrated conclusively that at least two forms of hominids were coeval.

Taxonomic questions arose (Oakley and Campbell 1964) over the relationship between *Homo habilis* and the South African form *Telanthropus capensis*, which had already been referred to as *Homo erectus* by Robinson (1961). These authors claimed that if *Homo habilis* proved to be conspecific with *T. capensis*, the name *capensis* would have priority over that of *habilis* but only for the genus *Australopithecus* as *capensis* was already occupied in the genus *Homo* through the actions of Broom when he earlier described a skull from Boskop, South Africa.

The relationship between *Homo habilis* and earlier and later forms was suggested by Montagu and Tobias (1965). Tobias was of the opinion that *H. habilis* stood intermediate in position between *Australopithecus* and *Homo erectus*, and believed that the interim solution of describing the specimen as a "lowly species" of *Homo* seems a reasonable compromise." Montagu, on the other hand, thought that *Homo habilis* could perhaps be more appropriately regarded as an early form of *Homo erectus*. Tobias (1966a, b) Leakey (1966, 1969) reargued this position and Tobias (1966b: 957) concluded that perhaps the more correct taxonomic label would be *Homo erectus habilis*. Leakey (1966: 1280), however, disagreed with Tobias in the *H. habilis* represented a stage in evolution from *A. africanus* to *H. erectus*, rather it seemed to him that *H. habilis* and *H. erectus*, as well as certain australopithecines, all represented distinct lineages by the early Pleistocene. *Homo erectus*, he believed, became extinct while *Homo habilis* subsequently gave rise to *Homo sapiens*.

Robinson (1966) again strongly disagreed claiming that the proponents of *Homo habilis* failed to treat variability in fossil forms adequeately or realistically and that the criteria which were used to sort *Homo habilis* from *Australopithecus* were not valid. His position was defended by Bielicki (1966), Brace (1968), and Simons, Pilbeam and Ettel (1969). The primary criticisms for *Homo habilis* given by Simons *et al*. (1969: 258-259) were that the Bed I material closely resembled *Australopithecus* sp. from South Africa and that the evidence suggested that Bed I *Homo habilis* should be grouped with *A. africanus*. The Bed II material, however, differs from Bed I material in size and morphological detail and resembled *Homo erectus* in certain morphological details. Additionally the material from these two deposits represent distinct temporal spans separate from on another by as much as a million years.

The problems involving the taxonomy from the remainder of the East African sites yielding fossil hominids has almost entirely been avoided due to the cautiousness of researchers in proposing new names. With two exceptions, the fossil hominids recovered from the depostis of Lake Rudolf and elsewhere have been grouped either within the genus *Homo* or within the genus *Australopithecus*. Arambourg and Coppens (1967) provisionally describe a mandible from the lower Omo Basin as *Paraustralopithecus aethiopicus* and Coppens (1965) suggested that a cranio-facial fragment from Chad which appeared similar to *Homo habilis* should be referred to as *Tchadanthropus uxoris*. Both names have not been well accepted by other investigators and may be considered obsolete.

The Usno and Shungura Formations of the lower Omo Basin yield a largely fragmentary fossil record of Hominidae extending from about 3 m.y. to 1 m.y. ago. Probably 4 hominid taxa are represented in this time range. *A. africanus* is characteristic of the nearly 3 to 2.5 m.y. time range and is persistent until about 1.9 m.y. A morphologically distinct but presumably related species; *A.* aff. *boisei*, or unknown origin appears about 2.1 m.y. and is evidence for upward of a million years unchanged in craniofacial morphology. Approximately 1.85 m.y. the first evidence of the genus *Homo* appears in upper member G and is comparable to samples of *Homo habilis*. Samples of *Homo erectus* have been uncovered in the uppermost units of member K, radiometrically dated to about 1.1 m.y. (Howell and Coppens, 1976).

From the earliest descriptions much of the East Rudolf material could be grouped with known samples of the robust australopithecine. However the contemporary occurrence of what R. Leakey (1971) described as members of the genus *Homo* was conclusively demonstrated (R.Leakey 1976a, b). Previously he has argued that the concept of the gracile australopithecine being ancestral to *Homo* would require reexamination and suggested, following Wolpoff and Brace, that the gracile variety may prove to be the female of the robust form.

It is obvious that there is extensive variability within the hominid sample. However, R. Leakey (1976a: 482) feels that there is some evidence to suggest three perhaps four separate lineages represented in the East Rudolf succession.

The robust australopithecine lineage found throughout the Koobi Fora Formation is represented by KNM-ER 406, the largest specimen in the sample. Within the Upper and Ileret members the occurrence of the genus Homo can be demonstrated with the mandibles KNM-ER 820 and 992 and in morphology resemble typical Homo erectus from elsewhere. In the Lower Members R. Leakey groups the Homo remains into two samples; one, which he calls the large form represented by KNM-ER 1470, 1590 and 1802, and a small form, represented by KNM-ER 1501 and 1503. The most complete cranium KNM-ER 1470 was claimed to be quite distinctive from Homo erectus in the form of the facial and maxillary regions. However, he did not relegate # 1470 to the taxon Homo habilis because the East Rudolf specimen was larger brained and came from a supposedly earlier time period (R. Leakey 1973). He later (R. Leakey 1976a) modified this position by stating that this material contrasted to other known forms of Homo except those specimens from Olduvai Gorge, OH 7, 16 (Homo habilis).

The evidence for the existence of the gracile australopithecine is mostly lacking. However, R. Leakey's (1974) study of the 1973 East Rudolf hominid collection revealed the presence of a hominine, KNM -ER 1813, whose dentition and cranial capacity appeared small. He compared these specimens with OH 24 and with material from Sterkfontein, and claimed that this specimen may demonstrate the presence of a third hominid lineage in the Lower Member. In addition he proposed a fourth line which he believed represented a remnant population of a primitive third genus of hominid. In this category he placed KNM-ER 1482 and the Omo mandible originally described as *Paraustralopithecus*.

Robinson (1972), claiming that R. Leakey had used the diagnostic features of *Paranthropus* as a working definition of "australopithecine" as a whole, questioned whether the known sample of hominids from East Rudolf is basically the same as the sample from South Africa. He believed that morphologically and adaptively the robust austraolpithecines in the two regions represent members of the same lineage, and that the smaller hominids, Leakey's *Homo* sp. and Robinson's *Homo africanus*, were basically of the same stock. Field work over the past several years ahs made it clear that at least two forms of hominid co-existed in Africa (Leakey and Walker, 1976): one generally recognized as the large form of australopithecine and the other an early member of the genus *Homo*. This picture has been confirmed by material from the Omo (Howell 1976) and the Hadar (Johanson and Taleb, 1976). R. Leakeys (1974) interpretation of the affinity of the fossil hominids at East Rudolf has suggested the prescence of possibly four contemporaneous hominids. Johnason and Taleb (1976) suggest possibly three at Hadar.

A recent suggestion was made that whatever the total number of contemporaneous hominid taxa, the record indicated not a simple progression of ancestor descendant populations, but rather a number of hominid radiations and adaptations to slightly differend econiches. Such radiations it is claimed are generally common during initial occupation of new habitats by immigrant populations and function in directing populations into available new niches. The claim is further made that this diversity in hominid forms suggest considerable antiquity for the human lineage with splits occurring at different times in response to different situation. This ultimately raises the problem of determining how many such econiches are available to hominids of a forest-margin / savannah ecozone.

Recently Campbell (1973) has proposed a revised taxonomy for fossil man in which he established two species of *Australopithecus* -- a large form, *boisei*, and the more gracile form, *africanus*. From the evidence of the post crania he claimed that both forms were bipedal and savannah adapted, but must have originally been geographically isolated to permit speciation. He believed that *A*. *boisei* could have occupied savannah regions of southern Eurasia, thereby competing with *Gigantopithecus*, and then secondarily occupied the grasslands in Africa. Campbell revises the status of the South African hominids by claiming that few meaningful distinctions can be made between the robust and gracile specimens and that both forms are actually represented in all deposits except Taung. For this reason he lumps all of the South African fossils into one category, *Australopithecus* *africanus*. Included also in this category is *Homo* *habilis* from Olduvai and KNM- ER 1470 from East Rudolf.

Campbell asserts that taxonomy should be based on chronology: *Australopithecus* should be retained as a taxonomic label for the early members of the lineage leading to modern forms. This genus was succeeded by the genus *Homo* in time at approximately 1.5-1.3 m.y. Generic distinction between the two forms is based, in his words, on " a whole series of related cultural developments based on language and technology which enabled the hominids to adapt to and survive in zones of low climatic equability" (Campbell 1973: 200).

FIGURE II- 36

Provisional Phylogenetic Trees of the Plio-Pleistocene Hominidae

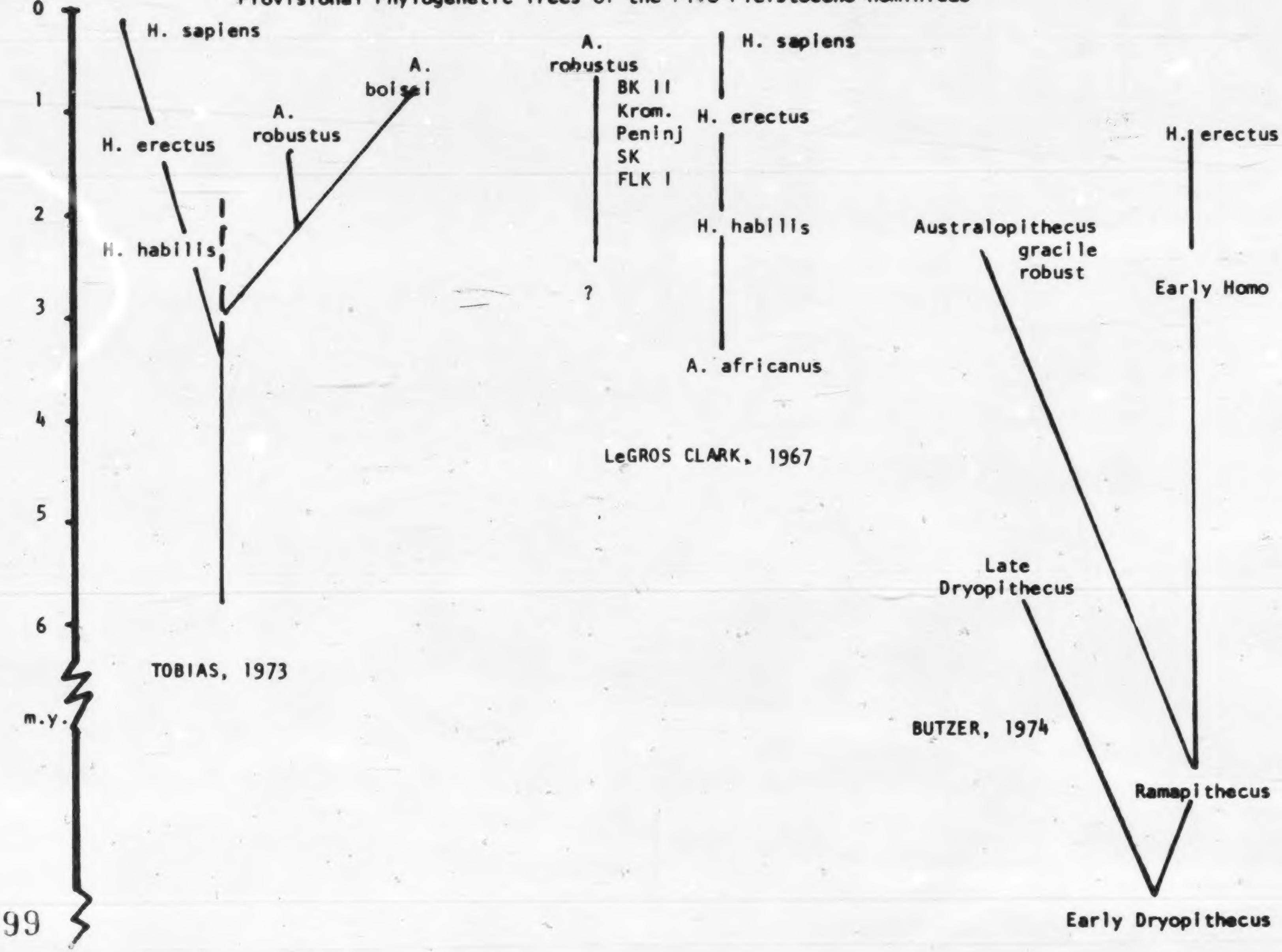

0
1
2
3
4
5
6
m.y.
H. sapiens
H. erectus
H. habilis
A. robustus
A. boisei
TOBIAS, 1973
A. robustus
BK II
Krom.
Peninj
SK
FLK I
?
H. sapiens
H. erectus
H. habilis
A. africanus
LeGROS CLARK, 1967
H. erectus
Australopithecus
gracile
robust
Early Homo
Late
Dryopithecus
BUTZER, 1974
Ramapithecus
Early Dryopithecus

FIGURE II-36 (Continued)

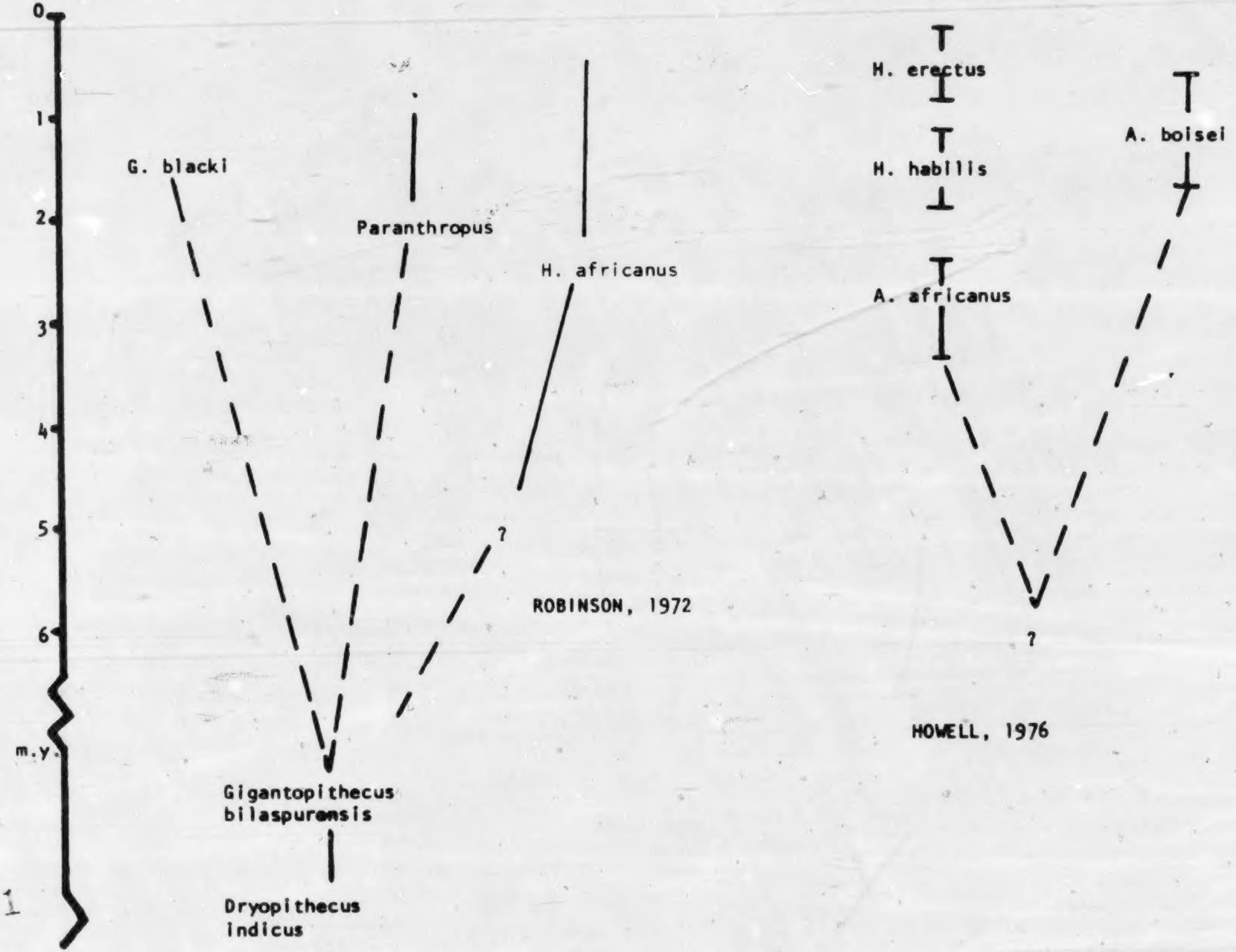
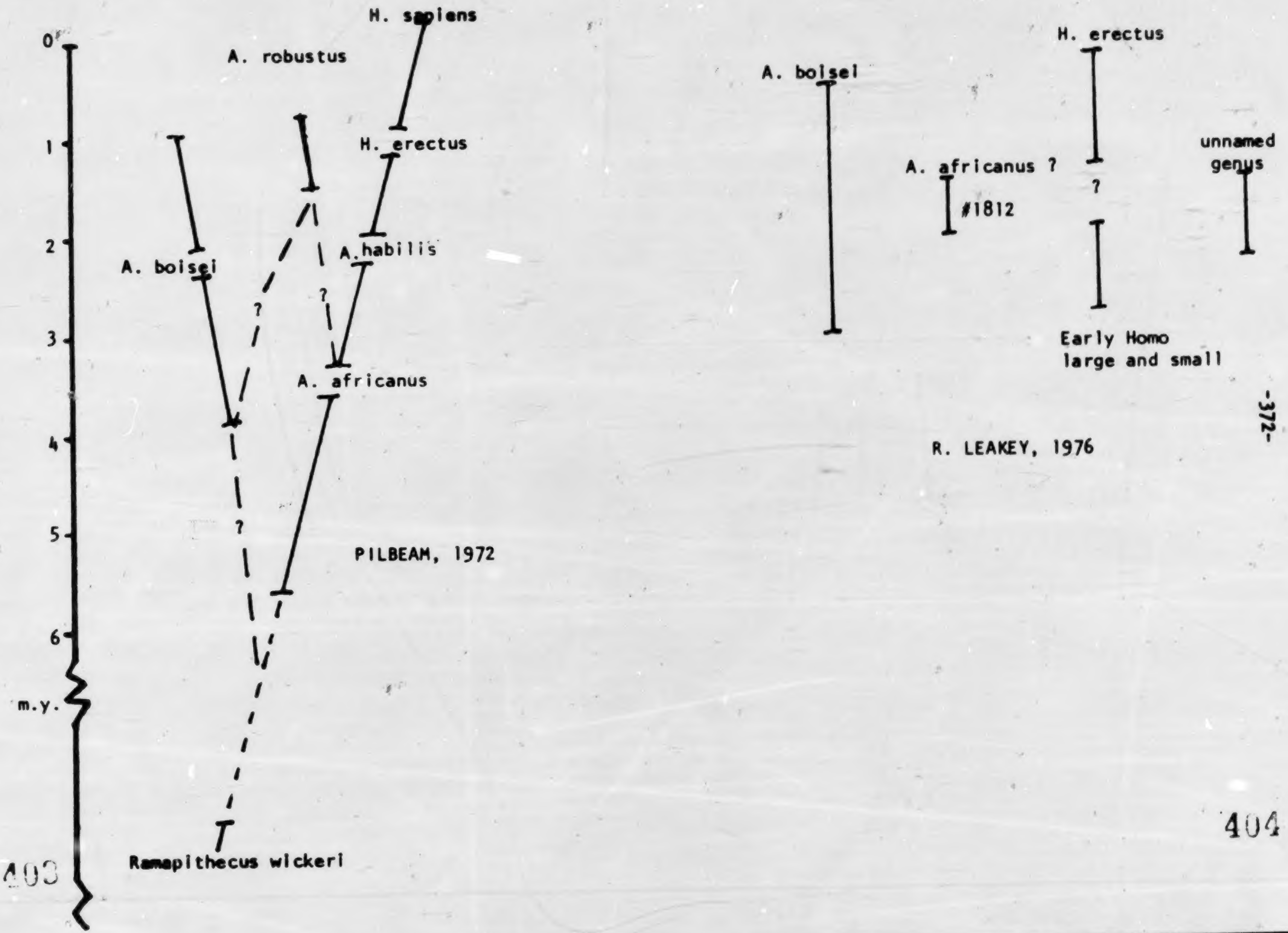

0
1
2
3
4
5
6
m.y.
G. blacki
Paranthropus
H. africanus
?
ROBINSON, 1972
Gigantopithecus
bilaspurensis
Dryopithecus
indicus
H. erectus
H. habilis
A. africanus
A. boisei
?
HOWELL, 1976

FIGURE II-36 (Continued)


H. sapiens
A. robustus
H. erectus
A. habilis
A. boisei
A. africanus
Ramapithecus wickeri
0
1
2
3
4
5
6
m.y.
?
?
?
PILBEAM, 1972
A. boisei
H. erectus
A. africanus ?
#1812
?
unnamed genus
Early Homo large and small
R. LEAKEY, 1976

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1971 New hominid skull from Bed I, Olduvai Gorge, Tanzania. Nature 232: 303-312.

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F. BIBLIOGRAPHY OF MIOCENE HOMINOIDS

BIBLIOGRAPHY OF MIOCENE HOMINOIDS

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1971 *Ramapithecus wickeri* mandible from Fort Ternan, Kenya. Nature 231: 192-194.

Describes the specimen (KNM FT 45) from Fort Ternan consisting of a portion of the left corpus of the mandible complete nearly to the midline of the symphysis, with crowns of both premolars. The body and symphyseal region is relatively low and robust. The morphology of the zygomatic proxess, maxilla and dentition suggest adaptation for powerful lateral grinding and claims that the east African and Indian forms of *Ramapithecus* are at least specifically distinct.

1974 New Species of *Dryopithecus* from Kenya. Nature 249: 188-190.

Abstract: Two new species of Pongidae, assigned to a new subgenus of *Dryopithecus*, are described. These assignations are based mainly on new specimens discovered recently in Kenya, but some other specimens are reassigned to the hypodigms of the new species. A more complete revision of the African early Miocene dryopithecines is in preparation. Photographs of the upper dentition of several species of dryopithecines and new mandible of *D. gordoni* are included as plates. Measurements of M^1 of *D. gordoni* and *D. vancouveringi* are included.

Conroy, G. C.

1972 Problems in the interpretation of *Ramapithecus* with special reference to anterior tooth reduction. AJPA 37: 41-47.

Tabulates 16 facial and dental characteristics which can be used to describe the hominid affinities of the *Ramapithecus* material. Defines relative anterior dental reduction as referring to the overall incisor size (area) as compared to an $M^1 + M^2$ area which he claims is reduced from *Ramapithecus* to *Homo* but is increased from *D. africanus* to *Pan*. Tables and ratios of tooth dimensions in fossil and recent hominids.

Couvering, J. A. van and J. A. Miller

1969 Miocene stratigraphy and age determinations, Rusinga Island, Kenya. Nature 221: 628-632.

Potassium/argon dating of the lavas of Rusinga Island indicate that most of the vertebrate fossils including *Kenyapithecus africanus* Leakey come from strata of the early Miocene of approximately 19 million years ago. Discusses the geological successions of the Rusinga Island deposits.

Frayer, D. W.
1973 *Gigantopithecus* and its relationship *Australopithecus*. AJPA 39: 413-426.

Abstract: *Gigantopithecus blacki* and *G. bilaspurensis* are compared to *P. gorilla* and *Australopithecus*. The total morphological pattern of *Gigantopithecus* mandibles is more similar to *Australopithecus* than to *Gorilla*. Two major points are raised. (1) *G. blacki* might be considered an aberrant hominid rather than an aberrant pongid. (2) *G. bilaspurensis* can be considered an equally likely candidate, along with *Ramapithecus*, for possible hominid ancestry. Comparision of teeth: *Gigantopithecus*, *Australopithecus*, and *Pan gorilla* (Table 1). Tooth measurements and indices for two East African australopithecines and *G. bilaspurensis* (Table 2). Length/breadth indices for lower molar of *G. blacki* and *G. bilaspurensis* and *Australopithecus*.

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The argument is proposed that *Kenyapithecus* is best interpreted as a representative of the rich variety of forms characteristic of the hominid adaptive radiation in Miocene times. The specimen does not have to be interpreted necessarily as a remote ancestor of man since many of the features shared with *Homo* may be parallelisms. Sees the loss of the cingulum in *Kenyapithecus* as precluding the ancestry of *Australopithecus*.

Greenfield, L.
1974 Taxonomic reassessment of two *Ramapithecus* specimens. Folia Primatologia 22: 97-115.

The author argues that two mandibles recently assigned to the genus *Ramapithecus* should be transferred back to the Dryopithecinae GSID 199, BM(NH) 15423). He claims that institial wear is a feature controlled by dental age and can be seen in hominids and fossil and recent pongids. It therefore has no taxonomic relevance The molar gradient steepness, mandibular corpus thickness, relative molar breadth, enamel thickening and third molar morphology are also all poor taxonomic markers and show that *Ramapithecus* does not differ significantly from Dryopithecine specimens.

Jolly, C. J.
1970 The seed-eaters: a new model of hominid defferentiation based on a baboon analogy. Man 5: 5-26.

Provides a new model for understanding hominid divergence based initially on a seed-eating econiche. Parallels may be seen in the Gelada baboon whose diet consists essentially of tough small objects. Views the robust australopithecines as representatives of Phase I adaptation, specialization related to the seed-eating complex. The gracile australopithecines, however, should be viewed as early Phase II representatives whose adaptations include recognizable culture, improved bipedalism and some cerebral expansion beyond that seen in the robust group. Favors sinking *Australopithecus* in *Homo* as suggested by Robinson (1965).

Kinzey, W. G.

1970 Basic rectangle of the mandible. Nature 228: 289-290.

Calculates an index for Leakey's basic rectangle of the mandible in which an attempt is made to show that *Kenyapithecus africanus* does not differ significantly from other early Miocene fossil apes.

1973 Ceboid models for the evolution of Hominoid dentition. Journal of Human Evolution 3: 193-203.

The presence of specializations for tough-object feeding in the arboreal cebids such as *Cebus apella* and *Callicebus* indicates that hominids may have acquired such specializations in an arboreal habitat before becoming terrestrial. Cites evidence of parallelisms in jaw shape, loss of cingulum and diet among some of the New World monkeys. Predicts that when postcrania of *Ramapithecus* are discovered that they will not show evidence of bipedal adaptations to a terrestrial environment.

Koenigswald, G. H. R. von

1952 *Gigantopithecus blacki* v. Koenigswald, a giant fossil hominoid from the Pleistocene of Southern China. Anthropological Papers of the American Museum of Natural History 43: 291-326.

Describes the history of the *Gigantopithecus* discoveries, lists of associated fauna, and the geology of various cave sites in Southern China yielding fossils of Pleistocene age. Describes the fossil material consisting of lower 3rd molars, 2nd premolars, upper 2nd molars, a central incisor and canines. Believes that *Gigantopithecus*, as well as *Australopithecus*, were overspecialized side branches of the human line.

1957 Remarks on *Gigantopithecus* and other hominoid remains from Southern China. Proceedings Kon Akad. Wet. 60: 153-159.

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1972 Not from the apes. New York: Pantheon Books, 183 pp.

Discusses the possibilities that man on the one hand and monkeys and apes on the other hand have been separate lineages for more than 35 million years, that monkeys and apes descended from the early ancestors of man and may be considered specialized forms, that most of man's history was spent in an arboreal habitat until some 5-10 million years ago, that man has repeatedly speciated all of which except one have become extinct through competition or direct conflict with one another, and that differences in sexual behavior have been overstressed. There may ahve been little absolute division of labor amongst the sexes.

Leakey, L.S.B.

1967 An early Miocene member of Hominidae. Nature 213: 155-163.

Describes the history of discoveries and controversies over the status of Kenyapithecus wickeri and new fossil species from Songhor and Rusinga Island of early Miocene age, named Kenyapithecus africanus, type specimen, a maxilla, described in 1951 by Le Gros Clark and Leakey as Sivapithecus africanus. Includes seven new specimens referred to as the new Kenyapithecus africanus species consisting of mandibles and maxillary fragments isolated teeth and part of a clavicle. Revises the earlier diagnosis for the genus Kenyapithecus Leakey 1961.

1968a Lower dentition of Kenyapithecus africanus. Nature 217: 827-830.

Describes a mandible with symphyseal region and teeth preserved from early Miocene deposits at Kathwange, Rusinga Island, Kenya. Specimens Rusinga (1967: 394) supposedly compares closely with other fossils previously described. Describes the morphology of the jaw and teeth between apes and man by the "basic rectangle of the mandible" and offers this as partial proof of the hominid status of K. africanus. Claims ancestry of the Kenyapithecus group in a pre-Miocene form of Proconsul.

1968b Bone smashing by late Miocene Hominidae. Nature 218: 528-530.

Describes fragmented bone assemblages from the Fort Ternan site, examples, the author claims, of depressed fractures "usually associated with a blunt instrument". Describes the recovery of a lave chunk exhibiting several battered edges, and with the appearance of having been used to smash bone. Suspects that Kenyapithecus was, by upper Miocene times, a tool user.

1969a Fort Ternan hominid . Nature 222: 1202

Argues that Simons' contention of the Fort Ternan fauna as an incursive group from Eurasia is incorrect. Questions the contemporaneity of the Chinji fauna of the Siwaliks, India, with that of Fort Ternan, Kenya.

1969b Ecology of North Indian Ramapithecus. Nature 223: 1075-1076.

Disagrees with Tattersall's paleoecological reconstruction of the Nagri Mio-Pliocene environment. Argues that most of the fossil faunal evidence can be argued favoring a more open country setting rather than tropical forest.

1970a The relationship of African apes, man, and Old World monkeys. Proceedings of the National Academy of Science 67: 746-748.

Disagrees with Wilson and Sarich (1969) on paleontological grounds that the superfamilies of mankeys and apes separated as late as 30 million years ago. Given if *Kenyapithecus wickeri* is a hominid then if the biochemical difference between monkey and man are as much as 6x, then the point of divergence between the two forms would be closer to 72 million years.

1970b "Newly" recognized mandible of *Ramapithecus*. Nature 225: 199-200.

Discusses the history behind the mandible recognized by Pilbeam (1969) as belonging to the genus *Ramapithecus*. The author claims that Pilbeam originally identified it as *Dryopithecus laietanus*, claims the specimen is too worn and weathered to make any generic or specific diagnoses and criticizes Pilbeam's criteria for placing it within the *Ramapithecus* group.

1971 Basic rectangle of the mandible in the Hominoidea. Nature 231: 60.

Argure for the acceptance of *Kenyapithecus africanus* into the family Hominidae based not only on the shape of the mandible but for a "large number of different characteristics to be seen in the specimens, every one of which is pointed in the same definite direction". Claims that resemblances between the pongid *Proconsul africanus* and the hominid *Kenyapithecus africanus* are to be expected considering both are close to the original common stock of both apes and man.

Pei, W. C.

1957 Discovery of *Gigantopithecus* mandibles and other material in Liu-Cheng district of central Kwangsi in South China. Vert. Palasiatica (Peking) 2: 65-72.

1962 Quaternary mammals from the Liu-Cheng *Gigantopithecus* cave and other caves of Kwangsi. Vert. Palasiatica 3: 211-218.

Pilbeam, D.

1966 Notes on *Ramapithecus*, the earliest known hominid, and *Dryopithecus*. AJPA 25: 1-5.

Describes the *Ramapithecus* specimens from India and East Africa and compares their morphology with the contemporary Dryopithecines. The remains of *Ramapithecus* resemble the equivalent parts of the later Hominidae and contrast with those of the Pongidae. *Ramapithecus* is the earliest known hominid, some 6 times older than the oldest Pleistocene forms. *Dryopithecus* is a pongid with three subgenera (*Dryopithecus*, *Proconsul* (Africa), and *Sivapithecus* (India)). *Proconsul* may be ancestral to the chimpanzee and the gorilla while *Sivapithecus* is ancestral to the orangutan.

1968 The earliest hominids. Nature 219: 1335-1338.

Discusses the main criteria for placing specimens within the family Hominidae, habitual bipedalism and presence of human dentition, and concludes that *Ramapithecus* was an early hominid even if evidence is produced which showed that it was not yet a habitual biped. Considers the position of a "Sivapithecus africanus" described by Leakey as an early Miocene hominid and concludes that it is much closer to *Dryopithecus* species than to *Ramapithecus*, and thus a pongid. States further that the Miocene fossil record indicates that hominids were recognizably distinct from pongids 14 million years ago.

1969 A newly recognized mandible of *Ramapithecus*. Nature 222: 1093-1094.

Announces the discovery of an additional mandible located in the fossil primate collections in the British Museum (Natural History) in London. Mandible BM(NH) 15423 was originally recovered from the deposits of Nagri (upper Miocene) at Domeli in the Salt Range. The mandible consisting of a left piece and most of the horizontal ramus is broken at the symphysis. The canine tooth is reduced and the posterior tooth row is crowded. The fore-shortened and deepened face and jaws suggests that *Ramapithecus* was capable of powerful chewing.

1970 *Gigantopithecus* and the origin of Hominidae. Nature 225: 516-519.

Describes the early history of *Gigantopithecus* discoveries and discusses the taxonomic arguments for and against including the species as a member of the family Hominidae. Discusses the new species of *Gigantopithecus* from India from middle Pliocene deposits and proposes a tentative phylogenetic sequence from *Dryopithecus indicus* (Late Miocene) to *D. giganteus* to *G. bilaspurensis* to *G. blacki*. Reviews the morphological trends within this lineage and compares the dental morphology to that of small object feeders such as *Theropithecus*.

Prasad, K. N.
1971 Ecology of the fossil Hominoidea from the Siwaliks of India. Nature 232: 413-414

Gives floral lists for fossils of the Nagri recovered from Haritalyangar and agrees broadly with Tattersall (1969) that the Nagri ecology was one of mixed forest interspersed with streams. Disagrees with Tattersall that the Nagri hominoids were not subjected to heavy predation by social carnivores.

Simons, E.L.
1961 The phyletic position of *Ramapithecus*. Postilla. Yale Peabody Museum No. 57: 1-9.

Discusses the significance of the type specimen of *Ramapithecus*, Y.P.M. 13799, consisting of the right maxilla including the alveoli of the upper incisors and canines, lacking only the upper 3rd molar. According to Simons, Lewis' (1934) conclusions of the hominid resemblances to *Ramapithecus* were correct and Hrdlick's (1935) rebuttal of the non-hominid characteristics was in error.

1964 On the mandble of *Ramapithecus*. Proceedings of the National Academy of Science 51: 528-535.

Describes newly assigned material to *Ramapithecus* consisting of second right maxilla from Haritalyangar (GSID 185), isolated upper incisor, and right and left horizontal rami of the same mandible (GSID 118, 119) described by Pilgrim as *Dryopithecus punjabicus* 1915, and as *Bramapithecus* by Lewis 1937. Claims the prior binomial for these forms must therefore be *Ramapithecus punjabicus*. Additional three specimens in the Yale Collections (13806, 13813, 13833). Molar teeth tend to be quadrate and crowded rather than anteroposteriorly elongate and spaced out as in *Dryopithecus*. Provides generic diagnosis for the genus *Ramapithecus*.

1969 Late Miocene hominid from Fort Ternan, Kenya. Nature 221: 448-451.

Arguments are presented to substantiate the author's claim that *Kenyapithecus wickeri* from East Africa should be placed as a junior synonym of *Ramapithecus*. Compares the fauna between Fort Ternan and the Chinji/Kamlial of India and claims that they are probably contemporary. Discusses morphological similarities between the two forms in the size of the upper central incisor teeth.

Simons, E. L. and D. Pilbeam
1965 Preliminary revision of the Dryopithecinae (Pongidae, Anthropoidea). Folia Primatologia 3: 81-152.

Revises the taxonomic relationships between the members of the family Pongidae and Hominidae (?). Concludes that the Miocene pongids can be considered as a single genus with three geographically divided subgenera: *Dryopithecus* (Europe), *Proconsul* (Africa), and *Sivapithecus* (India).

Tattersall, I.
1969a Ecology of North Indian *Ramapithecus*. Nature 221: 451-452.

Describes the environment in which *Ramapithecus* lived by comparing associated remains of the Nagri Fauna with modern tropical forms. Claims that despite a lack of abundant data the Nagri environment was one of broad rivers, bordered by tropical forests broken by the tree savannahs. Describes the ecological parallels with East Africa *Oreopithecus*.

1969b More on the ecology of North Indian *Ramapithecus*. Nature 224: 821-822.

Reiterates his previous arguments (contra Leakey 1969) for a forest-like environment for *Ramapithecus*. Claims that out of the many thousands of fossils which have come from numerous sites and at many levels within the Nagri Zone, very few are related to savannah-adapted forms. Compares the ecology of the Nagri with the earlier Chinji and later more arid Dhok Pathan.

Walker, A. and P. Andrews
1973 Reconstruction of the dental arcades of *Ramapithecus* *wickeri*. Nature 244: 313-314.

The author disputes the rounded dental arcade postulated from other reconstructions of *Ramapithecus* and argues its distinctness from the Dryopithecines. Reconstructs the shape of the mandible of *R. wickeri* (KNM FT 45) by mirror image replica technique and determines that the specimen had very small anterior teeth, as well as posteriorly diverging and nearly straight cheek tooth rows rather than widely separated and curved tooth rows of modern man. The palate is narrow, the premaxillary region abbreviated and the face broad and flat.

Woo, J. K.
1962 The mandibles and dentition of *Gigantopithecus*. Palaeontologia Sinica 11: 1-94.

Yulish, S.M.
1970 Anterior tooth reductions in *Ramapithecus*. Primates 11: 255-263.

Contends that the criteria of anterior tooth height reduction for *Ramapithecus* is not well founded and not significantly different from modern pongids, and therefore the classification of FT 1271 as a hominid is unjustified on this criteria alone. provides metrical data on maxillary dentition in *Pan*, *Gorilla* and *Homo* *sapiens*.

Zwell, M.
1972 On the supposed "Kenyapithecus africanus" mandible. Nature 240: 236-238.

Analysis of KNM RU 2087, described by its author L.S.B. Leakey in 1968 as *Kenyapithecus* *africanus*. This author explains why he feels this specimen is a dryopithecine. Includes bivariate plots of the lower teeth and a comparison of hominid and pongid characters.